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

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Abstract

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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)."

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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 & Schmahmann, 2010; Mariën et al., 2001). Anatomically, projections between the

1 cerebral and cerebellar cortices are largely (though not exclusively) contralateral
2 (e.g., Brodal, 1979). The lateralization is also supported by fMRI findings that
3
4 linguistic functions are mainly localized in the right hemisphere of the
5
6 cerebellum, though often involving a small component of the contralateral lobule
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8 (e.g., Stoodley & Schmahmann, 2009). Finally, most clinical reports suggest that
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10 language impairments such as impaired verbal fluency and agrammatism
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12 generally arise following right cerebellar hemisphere lesions (Gebhart et al.,
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14 2002; Hassid, 1995; Hokkanen et al., 2006; Marien et al., 2001; Riva and Giorgi,
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16 2000; Silveri et al., 1994; Zettin et al., 1997; Scott et al., 2001). In this context, it
17
18 should be mentioned that a small number of neuropsychological studies have
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20 also reported linguistic deficits following left cerebellar hemisphere lesions (e.g.,
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22 Fabbro et al., 2000; Cook et al., 2004; Murdoch & Whelan, 2007). Though one
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24 possibility is that the pathophysiological mechanism underlying these lesions
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26 was crossed cerebellocerebral diaschisis (e.g., Cook et al., 2004), it is equally
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28 possible that they reflect ipsilateral cerebellar cerebral diaschisis, implying that
29
30 the cerebellum might be bilaterally involved in language processing (Murdoch &
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32 Whelan, 2007). Another exception to the lateralization of linguistic function is to
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34 be found in prosodic and auditory language processing, that both seem to be left
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36 lateralized within the cerebellum (e.g., Callan et al., 2007; Petacchi et al., 2005).
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38 These latter findings suggest an even more fine-grained functional cerebellar
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40 specialization mirroring the cortical hemispheric specialization. Nevertheless,
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42 though the involvement of the left cerebellar hemisphere in linguistic function
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44 certainly merits further investigation, the global impression provided by the
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46 previous literature, especially in what concerns the cognitive components of
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1 language production, is that the right hemisphere has a predominant, though not
2 exclusive, role for linguistic functions.
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5 In sum, the combination of these two topographic functional distinctions
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7 leaves posterior lobules VI and Crus I and II in the right cerebellar hemisphere as
8
9 prime candidates for hosting processes of language production beyond its pure
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11 motor aspects. A further question is exactly what type of cognitive function(s)
12
13 the cerebellum is involved in. Concerning language, this function should be
14
15 rather indirect (i.e., not directly concerning linguistic representations or their
16
17 access) since damage to the cerebellum is not strongly tied to central
18
19 disturbances of production and comprehension (e.g., Ito, 2008; Desmond & Fiez,
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21 1998). More generally, several authors highlight that although many functions
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23 have been ascribed to the cerebellum, the uniformity of its synaptic organization
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25 suggests that a single, characteristic computation may be common to all (e.g.,
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27 Medina & Mauk, 2000). This hypothesis of neural computation homogeneity has
28
29 lent itself to hypotheses of cognitive computation homogeneity across different
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31 regions of the cerebellum (i.e., motor and cognitive regions). One example of this
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33 which we will focus on in the present study is that the cerebellum is devoted to
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35 internal modeling of self-generated actions, whether motor or cognitive in
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37 nature (e.g., Ito, 2008).
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49 1.2 Internal modeling of upcoming speech 50

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

1 through the cerebellum. Empirical evidence suggestive of a role for internal
2 modeling of articulation actions (i.e., detecting and correcting errors in the
3 programming and execution of speech articulation) can be found in the literature
4 (e.g., Houde, Nagarajan, Sekihara, & Merzenich, 2002; Heinks-Maldonado,
5 Mathalon, Gray, Ford, 2005; Ghosh, Tourville, & Guenther, 2008). More
6
7 hypothetical and less explored is the hypothesis that also levels beyond pure
8 motor aspects of language might be monitored through internal models as
9 proposed by Pickering and Garrod (e.g., Alario & Hamamé, 2013; Hartsuiker,
10 2013; Pickering & Garrod, 2013; Pickering & Garrod, 2014; Strijkers, Runnqvist,
11 Costa & Holcomb, 2013). Given the above-mentioned (section 1.1) lack of central
12 disturbances following cerebellar lesions, one might wonder whether it makes
13 sense to hypothesize about cerebellar involvement in such a general mechanism
14 as internal modeling. However, internal modeling of upcoming speech, while
15 indeed being a mechanism of a general nature in the sense that it is supposed to
16 always co-occur with the preparation of speech, is arguably a process whose
17 incorrect functioning could be difficult to detect in comparison with many other
18 components of language processing. This is because the consequences of internal
19 modeling only become apparent when the speaker is preparing an erroneous
20 utterance, which is not the default situation. In contrast, other general processes
21 such as lexical access, phonological and phonetic encoding etc. are not only
22 always present during language processing, but they are essential to it as no
23 language comprehension/production can take place without them. Elsewhere it
24 has been argued that high-level linguistic disturbances subsequent to cerebellar
25 lesions may be more accurately detected and characterized by high-level
26 assessments that evaluate the proficiency of more complex language processes
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1 beyond single word hierarchies (Murdoch, 2010). Such high-level assessments
2 would consist in tasks demanding frontal lobe support in the manipulation of
3 novel situations, lexical- semantic operations, the development of language
4 strategies, and the organization and monitoring of responses (Copland et al.,
5 2000). As we will describe below, our experimental task was designed keeping in
6 mind this potential difficulty of detecting internal modeling functioning.
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17 Insert Figure 1 about here
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19 1.3 The current study 20

21 Here we wanted to test whether monitoring language production levels
22 beyond pure motor aspects of speech is achieved through internal modeling, and
23 whether the cerebellum has a necessary role in such modeling. We used
24 repetitive transcranial magnetic stimulation rTMS at a frequency of 1Hz, which is
25 known to temporarily inactivate the stimulated area. Guiding our predictions by
26 the two functional topographic distinctions reviewed above, we expected that
27 disrupting cerebellar function in the right posterior lobules Crus I and II might
28 lead to an impaired speech production monitoring (see Figure 1a). As a control
29 condition (and in counterbalanced orders), the same participants received
30 stimulation to the contralateral area in the left hemisphere of the cerebellum,
31 which should be less related to the linguistic processing of language production.
32 Participants engaged in a speeded language production task designed to prime
33 the production of errors (see Figure 1b). By creating a situation of high load on
34 the speech production monitor through the speeded nature of the task and by
35 priming speech errors, we aimed at providing the ideal circumstances for
36 observing a high-level linguistic impairment that would most probably be
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1 undetectable with standard language test batteries (e.g., Copland et al., 2000;
2 Murdoch, 2010). To have an additional marker of self-monitoring beyond global
3 error rates, we manipulated the lexical status of the primed error outcomes.
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5 Previous research has shown that speakers are more likely to produce errors
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7 resulting in new words than pseudowords, indicating that lexicality is a filter
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9 used to intercept errors during speech production (Baars, Motley, & MacKay,
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11 1975; Hartsuiker, Corley & Martensen, 2005; Nootboom, 2005). Returning to
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13 our task, the following three predictions can be made: 1) Impaired language
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15 processing of any sort (including monitoring) would be apparent through slower
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17 response times and/or higher error rates; 2) Impaired self-monitoring for
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19 accuracy would be indexed by an overall increased error-rate; 3) Impaired self-
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21 monitoring for lexicality would result in a modulation of errors as a function of
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23 their lexical status.
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31 2. Methods

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35 The study received appropriate ethical approval (filed under “ID-RCB-
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37 2009-A01059-48” at “Comité de Protection des Personnes Sud Méditerranée I”)
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39 and was performed in accordance with the declaration of Helsinki.
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41 2.1. Participants

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44 Sixteen (ten females, six males) right-handed native speakers of French
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46 took part in the study in exchange for a monetary compensation. The average age
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48 of participants was 24 (SD 3), with an average of 16 (SD 2) years of education. No
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50 participant reported any history of language or neurological disorders.
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52 2.2. Materials

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55 Target stimuli consisted of 160 printed French words (see appendix A). For
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57 illustrative purposes the examples in the text are given in English. Across
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1 subjects, each word was used twice in combination with another word (e.g., *mole*
2 *sail*, *mole fence*). When exchanging the first letters of these combinations, one of
3
4 them resulted in a new word pair (*sole mail*, lexical error outcome) and the other
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6 in a non-word pair (*fole mence*, non-lexical error outcome). All combinations for
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8 which initial sound exchange resulted in new word-pairs (*mole sail*) were used
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10 also in the exchanged format (*sole mail*). A given subject was only presented with
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12 one combination for each word (lexical or non-lexical outcome), and was only
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14 presented with one of the words differing in only the first sound (*mole* or *sole*).
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16 This resulted in the creation of four experimental lists with 80 word pairs (40
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18 lexical and 40 non-lexical error outcome). Each subject received one such list
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20 divided in two separate blocks of 40 pairs each (20 lexical and 20 non-lexical
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22 outcome). Stimuli pertaining to the two blocks were matched for lexical
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24 frequency of the first word in the combination, overall lexical frequency,
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26 neighborhood density, word length, and phonetic distance.
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35 During the experiment, each target word combination was preceded by
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37 three priming word pairs. The first two shared the initial consonants and the
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39 third pair had further phonological overlap with the error being primed (*sun*
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41 *mall* – *sand mouth* – *soap mate* – *mole sail*). In each of the two experimental
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43 blocks, subjects were also presented with 70 filler pairs that had no specific
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45 relationship to the target pairs. One to three such filler pairs were presented to
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47 subjects before each sequence of primes and target. Thus, each subject was
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49 presented with 460 unique word combinations divided in two blocks of 230
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51 word pairs each (40 targets, 120 primes and 70 fillers). Each experimental block
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53 contained three sub-blocks in which these 230 words were repeated three times
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55 in different orders. Subjects were instructed to read all target word pairs aloud,
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1 all prime pairs silently, 41% of the filler pairs aloud, and 59% of the filler pairs
2 silently.
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4 2.3. Procedure

5 2.3.1. *Pre-stimulation protocol.*

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7 Participants first received written and oral information about the rTMS
8 technique, and they underwent a brief examination by a neurologist. They were
9 then asked to fill in a questionnaire and sign an informed consent. Next, they
10 were familiarized with the experimental task through written and oral
11 instructions and through several practice trials.
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22 2.3.2. *rTMS protocol.*

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

1 besides serving as a control for any non-specific effects of the stimulation, it also
2 keeps the variable of physical discomfort constant across conditions. This is
3
4 especially important since cerebellar TMS has been reported to induce muscle
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6 discomfort and twitching (e.g., Théoret et al., 2001; Harrington & Hammond-
7
8 Tooke, 2015), making it difficult to dissociate any impact on behavior from a
9
10 general attention decline induced by this discomfort. Repetitive transcranial
11
12 magnetic stimulation (rTMS) was effectuated with a figure-of-eight coil at 1Hz at
13
14 60% of maximum stimulator output intensity, using a Medtronic Magpro X100
15
16 TMS system. Each session was carried out in two parts: (1) 15 min stimulation
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18 (900 pulses) followed by 3*5 min of experimental task; (2) 15 min stimulation
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20 (to the opposite hemisphere) followed by 3*5 min of experimental task. The
21
22 order of stimulation (left/right first) was counterbalanced across participants.
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24 The duration of the off-line effects of low frequency rTMS is estimated to be
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26 between 60 and 100% of the duration of the stimulation (e.g., Nyffeler et al.,
27
28 2006; Eisenegger et al., 2008; Chen et al., 1997). This means that we could be
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30 rather confident that the effects of inactivation would last between 9-15 minutes
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32 of the experimental task following the stimulation of each hemisphere, and that
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34 the effects of stimulating one hemisphere would not carry over to performance
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36 on the experimental task after stimulating the other hemisphere.

47 *2.3.3. Experimental task protocol.*

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49 Participants wore headphones and they were told to silently read word
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51 pairs, but to name aloud the last word pair they had seen whenever an
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53 exclamation mark was presented. All targets and 41% of the filler items were
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55 followed by an exclamation mark presented for 500 ms. Each word pair was
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57 presented for 700 ms and was followed by a blank screen for 200 ms. In order to
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1 encourage participants to speak fast, a tone sounded 500 ms after the
2 presentation of the exclamation mark. The next item was presented 1000 ms
3 after the beginning of the tone. Stimulus presentation was controlled using
4 Eprime software. Productions were recorded both through Eprime and with a
5 separate recorder and were processed off-line.
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11 2.4. Data processing

12 2.4.1. Errors.

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17 A person naïve to the purpose of the experiment transcribed
18 orthographically all productions. The transcriptions were scored as correct,
19 errors, partial responses (e.g., only one word produced), dysfluencies or
20 omissions. The errors were classified as “priming related errors” or “other
21 errors”. “Priming related errors” included full exchanges (*mole sail => sole mail*),
22 partial exchanges (anticipations, e.g., *mole sail => sole sail*, perseverations, e.g.,
23 *mole sail => mole mail*, other partial exchanges, e.g., *mole sail => sole saint*),
24 repaired and interrupted exchanges (*mole sail => so...mole sail*), full and partial
25 competing errors (*mole sail => star milk/star sail*), and other related errors (*mole*
26 *sail => mail sole*). “Other errors” included diverse phonological substitutions that
27 were unrelated to the priming manipulation (e.g., *mole sail => hole saint/ro..mole*
28 *sail/...saint*).
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46 2.4.2. Response times.

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49 Another person naïve to the purpose of the experiment measured the
50 response times for all individual recordings using the software check-vocal
51 (Protopapas, 2007).
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57 2.5. Statistical analyses

1 The data were analyzed using the lme4 package (Bates et al., 2015) in R
2 version 3.2.2 (R Development Core Team, 2015). Errors were analyzed using
3 generalized linear mixed models (GLMM) with a binomial link function (e.g.,
4 Jaeger, 2008), estimating the conditional probability of a response given the
5 random effects and covariate values. Response times were analyzed with linear
6 mixed models (LMM), estimating the influence of fixed and random covariates on
7 the response. One difference between GLMMs and LMMs concerns the type of
8 hypothesis testing that can be used, which is related to the knowledge about the
9 dispersion parameter in both cases. In GLMMs of binomial data, the dispersion
10 parameter is fixed at 1 (e.g., Chen & Conomos, 2015), while in linear mixed
11 models the residual variance has to be estimated. For this reason, z-scores can be
12 used in GLMMs while t-values are used in LMMs. Because both z-scores and p-
13 values are related to the standard normal distribution, p-values can reliably be
14 obtained from z-scores. The summary output of the GLMM function of lme4 in R
15 provides p-values based on asymptotic Wald tests, which is common practice for
16 generalized linear models (e.g., Bolker et al., 2009). The Wald statistic is
17 asymptotically distributed as a standard normal distribution and uses the z-
18 score to calculate the p-value. In contrast, the summary output of the LMM
19 function only provides t-values. Consequently, we report p-values for error-rates
20 and t-values for response times. Following common practice (e.g., Fisher 1925),
21 we take t-values to approximate z-scores and assume that absolute values above
22 1.96 reflect significant effects.

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

1 variables was entered into the analysis individually, followed by interaction
2 terms, and only variables or interaction terms that were significant (i.e., with a T-
3 value above 1.96 or a p-value below .05) were kept in the analyses. In those cases
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5 value above 1.96 or a p-value below .05) were kept in the analyses. In those cases
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7 where a newly added variable was significant and changed the significance of
8
9 another variable, the anova function of R was used to compare both models and
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11 non-significant p-values were taken to indicate that the more parsimonious
12
13 model should be preferred.
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17 In all models, Participants and Items were included as crossed random
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19 effects (i.e., intercept estimates), allowing to tease apart the influence of
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21 subjects/items on their repeated observations from the influence of the fixed
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23 effects of theoretical interest. Errors (i.e., both related and other errors) were
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25 fitted with a first series of models to evaluate a non-specific impairment of self-
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27 monitoring after right hemisphere stimulation. These models included the fixed
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29 factors hemisphere and block. Next, the subset of priming-related errors were
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31 fitted in separate models to evaluate the output-tied lexicality bias (i.e., the
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33 tendency to make more lexical than non-lexical errors) and its interaction with
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35 hemisphere. These models thus included the fixed factors lexicality, hemisphere,
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37 and block.
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44 For response times, a Box–Cox test (Box & Cox, 1964) indicated that a
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46 logarithmic transformation was the most appropriate to approximate a normal
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48 distribution, and this is what was used. For clarity, however, we also report
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50 approximate estimates of the effect sizes in milliseconds obtained by running
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52 identical models with the untransformed response times. The fixed factors
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54 included in the models were hemisphere and block as well as the interactions.
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59 2.6. Results

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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.

Block	Right hemisphere			Left hemisphere		
	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 (1.5)	2.2 (0.8)	5.0 (0.9)	5.6 (1.3)	2.5 (0.9)	4.1 (0.8)
3	5.6 (1.3)	2.5 (0.9)	4.1 (0.8)	4.4 (1.1)	1.3 (0.6)	2.8 (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

1 global error-rates, we manipulated the lexical status of the potential error
2 outcomes (pseudoword errors are intercepted more often than word errors).
3
4 The following three predictions were made: 1) Impaired language processing of
5 any sort (including self-monitoring) would be apparent through slower response
6 times and/or higher error rates; 2) Impaired self-monitoring for accuracy would
7 be indexed by an overall increased error-rate; and 3) Impaired self-monitoring
8 for lexicality would result in a modulation of errors as a function of their lexical
9 status. In line with our first two predictions, we observed that after stimulation
10 to the right hemisphere of the cerebellum compared to the left hemisphere,
11 participants committed more errors (all three blocks) and took longer in starting
12 to produce correct responses (first block). Contrary to our third prediction, this
13 effect was independent of the lexical status of the error outcome (this non-
14 confirmed prediction will be further discussed below).
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32 In general terms, an implication of the right cerebellar lobules Crus I and II
33 in cognitive aspects of language production had already been highlighted by
34 functional activation studies and neuropsychological studies (e.g., Stoodley &
35 Schmahmann, 2009; Mariën et al., 2001). An important contribution of our study
36 is that it shows within the same participants that this area has a causal role in
37 language production, and that in a context in which compensatory changes or
38 rewiring has not had a chance to occur (e.g., as might occur following a stroke).
39 Furthermore, by including a dependent variable (error-rates) that can be directly
40 linked to a particular (though admittedly broad) cognitive process (self-
41 monitoring), this study helps constraining the functional role that the cerebellum
42 might have in the process of producing language. It should be noted that an
43 increase in response times as observed in the first block is also consistent with
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1 an impaired self-monitoring ability: for example, a delay in the interception and
2 inner repair of speech errors might lead to such a pattern. However, though
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4 parsimony favors a common origin of the increased error-rates and the response
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6 time delay, other possible accounts such as impairment in the temporal
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8 organization of the sound structure of utterances (e.g., Ackermann et al., 2007)
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10 remain equally possible for the response time delay.
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14 Theoretically, these data are consistent with the view that internal models
15 are used to self-monitor speech production (e.g., Pickering & Garrod, 2013;
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17 Pickering & Garrod, 2014; Hickok, 2012). In what follows we will try to shed
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19 some light at the issue of what level(s) of language production might be subject
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21 to this internal modeling. A first candidate level, which would not assume the
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23 current results to reflect the involvement of any linguistic processing proper, is
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25 articulation. Trouble with the control of motor production might indeed lead to
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27 certain speech errors in the form of pure dysfluencies or mispronunciations,
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29 though many problems of speech motor control will rather be reflected in
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31 properties that do not affect accuracy such as lengthening of certain segments,
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33 vocal quality, pitch, tone, volume, strength, steadiness, speed etc. However, the
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35 errors included in our analyses involved *phonological* units (speakers added,
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37 deleted, or exchanged phonemes), which, in our opinion, is not predicted by an
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39 impaired motor control function. Furthermore, speech motor control is not
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41 expected to be affected by the stimulation to Crus I and II of the right hemisphere
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43 (e.g., Stoodley and Schmahmann, 2009). Disorders related to articulatory aspects
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45 of language production such as dysarthria has been shown to involve lesions in
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47 the upper paravermal region of the right cerebellar hemisphere, the site of
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49 coordination of articulatory movements of the tongue and orofacial muscles (e.g.,
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1 Ackermann et al., 1992; Urban et al., 2003). Even though TMS lacks focal
2 precision at the millimeter level as discussed previously (section 2.3.3), the
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4 posterior areas we targeted here should be at a sufficient distance from the
5
6 anterior regions responsible for speech motor control.
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10 A second candidate level to locate our effects can be found moving a little
11 further along the cognitive continuum of language production. As mentioned in
12 the Introduction (1.2), the language production model of Hickok (2012)
13 conceives a role of the cerebellum for the internal modeling of phonetic aspects
14 of language production. However, this explanation is not satisfactory either to
15 account for the observed error pattern involving phonological units.
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24 Finally, moving upwards in the cognitive continuum of language
25 production, also a third candidate level can be excluded since we found no
26 evidence for an implication of the cerebellum in the monitoring of lexical
27 processing. That is, speakers intercepted and repaired internally non-lexical
28 items about to be produced to the same extent regardless of stimulation site. Of
29 course, being based on a null effect, this interpretation should be taken with
30 caution. In sum, our data suggest that the cerebellum, besides having a role for
31 speech motor control of phonetic aspects of speech, is also implicated in the
32 supervision of phonological aspects but not of higher levels of language
33 production.
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49 One possibility is that our findings reflect a difficulty of maintaining a
50 phonological speech goal (i.e., auditory target in terminology of Hickok, 2012),
51 perhaps due to interference with verbal working memory. That is, the referent of
52 comparison in the internal modeling process might be more easily disrupted
53 because of verbal working memory failure, resulting in phonological errors of
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1 both lexical and non-lexical types going undetected. Supporting this
2 interpretation is the fact that selective activation in tasks involving verbal
3 working memory in conjunction with language has been reported in posterior
4 parts of the cerebellum, predominantly in the right hemisphere, within a
5 network that also involves Broca's area and the supplementary motor area
6 (SMA) (e.g., Desmond & Fiez, 1998). Desmond and Fiez propose that the
7 cerebellum might serve to enhance working memory performance by comparing
8 the output of subvocal articulation with acoustically based phonological
9 representations in a short-term store. This is supposed to occur especially as the
10 memory load increases and the need for more accurate and efficient rehearsal
11 becomes more critical, as was presumably the case in our study in which
12 speakers were instructed to say aloud the latest word pair they had read
13 whenever an unpredictable beep sounded. Relevant for the ability of self-
14 monitoring, discrepancies between actual versus intended motor trajectories are
15 hypothesized to result in an error-correction that would serve to maintain the
16 integrity of the rehearsed items. (e.g., Desmond et al., 1997; Desmond & Fiez,
17 1998). This interpretation suggests that an accurate model of language
18 production and self-monitoring should integrate both domain-general cognitive
19 computations such as internal modeling, and interfacing cognitive systems such
20 as verbal working memory.

4. Conclusion

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

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

- 1
2 Ackermann, H., Mathiak, K., & Riecker, A. (2007). The contribution of the cerebellum to
3
4 speech production and speech perception: clinical and functional imaging data.
5
6 *The Cerebellum*, 6(3), 202-213.
7
8
9 Ackermann, H., Vogel, M., Petersen, D., & Poremba, M. (1992). Speech deficits in
10
11 ischaemic cerebellar lesions. *Journal of Neurology*, 239(4), 223-227.
12
13
14 Alario, F. X., & Hamamé, C. M. (2013). Evidence for, and predictions from, forward
15
16 modeling in language production. *Behavioral and Brain Sciences*, 36(04), 348-
17
18 349.
19
20
21 Andreasen, N. C., & Pierson, R. (2008). The role of the cerebellum in
22
23 schizophrenia. *Biological Psychiatry*, 64(2), 81-88.
24
25
26 Argyropoulos, G. P. (2011). Cerebellar theta-burst stimulation selectively enhances
27
28 lexical associative priming. *The Cerebellum*, 10(3), 540-550.
29
30
31 Argyropoulos, G. P., & Muggleton, N. G. (2013). Effects of cerebellar stimulation on
32
33 processing semantic associations. *The Cerebellum*, 12(1), 83-96.
34
35
36 Argyropoulos, G. P. (2015). The cerebellum, internal models and prediction in 'non-
37
38 motor' aspects of language: A critical review. *Brain and Language*.
39
40
41 Baars, B. J., Motley, M. T., & MacKay, D. G. (1975). Output editing for lexical status in
42
43 artificially elicited slips of the tongue. *Journal of Verbal Learning and Verbal*
44
45 *Behavior*, 14(4), 382-391.
46
47
48 Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modeling with
49
50 crossed random effects for subjects and items. *Journal of Memory and*
51
52 *Language*, 59(4), 390-412.
53
54
55 Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., ... &
56
57 Rcpp, L. (2015). Package 'lme4'. *Convergence*, 12, 1.
58
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51
52
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55
56
57
58
59
60
61
62
63
64
65
- Blakemore, S. J., & Sirigu, A. (2003). Action prediction in the cerebellum and in the parietal lobe. *Experimental Brain Research*, *153*(2), 239-245.
- Blakemore, S. J., Wolpert, D. M., & Frith, C. D. (1998). Central cancellation of self-produced tickle sensation. *Nature Neuroscience*, *1*(7), 635-640.
- Blakemore, S. J., Frith, C. D., & Wolpert, D. M. (2001). The cerebellum is involved in predicting the sensory consequences of action. *Neuroreport*, *12*(9), 1879-1884.
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in ecology & evolution*, *24*(3), 127-135.
- Box, G. E., & Cox, D. R. (1964). An analysis of transformations. *Journal of the Royal Statistical Society. Series B (Methodological)*, 211-252.
- Brasil-Neto, J. P., Cohen, L. G., Panizza, M., Nilsson, J., Roth, B. J., & Hallett, M. (1992). Optimal focal transcranial magnetic activation of the human motor cortex: effects of coil orientation, shape of the induced current pulse, and stimulus intensity. *Journal of Clinical Neurophysiology*, *9*(1), 132-136.
- Brodal, P. (1979). The pontocerebellar projection in the rhesus monkey: an experimental study with retrograde axonal transport of horseradish peroxidase. *Neuroscience*, *4*(2), 193-208.
- Callan, D., Kawato, M., Parsons, L., & Turner, R. (2007). Speech and song: The role of the cerebellum. *The Cerebellum*, *6*(4), 321-327(7).
- Chen, R., Classen, J., Gerloff, C., Celnik, P., Wassermann, E. M., Hallett, M., & Cohen, L. G. (1997). Depression of motor cortex excitability by low-frequency transcranial magnetic stimulation. *Neurology*, *48*(5), 1398-1403.
- Chen, H., & Conomos, M. P. (2015). GMMAT: Generalized linear Mixed Model Association Tests Version 0.6.

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64
65
- Cook, M., Murdoch, B., Cahill, L., & Whelan, B. M. (2004). Higher-level language deficits resulting from left primary cerebellar lesions. *Aphasiology*, *18*(9), 771-784.
- Desmond, J. E., Gabrieli, J. D., Wagner, A. D., Ginier, B. L., & Glover, G. H. (1997). Lobular patterns of cerebellar activation in verbal working-memory and finger-tapping tasks as revealed by functional MRI. *The Journal of Neuroscience*, *17*(24), 9675-9685.
- Desmond, J. E., & Fiez, J. A. (1998). Neuroimaging studies of the cerebellum: language, learning and memory. *Trends in Cognitive Sciences*, *2*(9), 355-362.
- Desmond, J. E., Chen, S. H., & Shieh, P. B. (2005). Cerebellar transcranial magnetic stimulation impairs verbal working memory. *Annals of Neurology*, *58*(4), 553-560.
- Dum, R. P., & Strick, P. L. (2003). An unfolded map of the cerebellar dentate nucleus and its projections to the cerebral cortex. *Journal of neurophysiology*, *89*(1), 634-639.
- Eisenegger, C., Treyer, V., Fehr, E., & Knöch, D. (2008). Time-course of “off-line” prefrontal rTMS effects—a PET study. *Neuroimage*, *42*(1), 379-384.
- Fabbro, F., Moretti, R., & Bava, A. (2000). Language impairments in patients with cerebellar lesions. *Journal of Neurolinguistics*, *13*(2), 173-188.
- Fisher, R. A. (1925, July). Theory of statistical estimation. In *Mathematical Proceedings of the Cambridge Philosophical Society* (Vol. 22, No. 05, pp. 700-725). Cambridge University Press.
- Gebhart, A. L., Petersen, S. E., & Thach, W. T. (2002). Role of the posterolateral cerebellum in language. *Annals of the New York Academy of Sciences*, *978*(1), 318-333.

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63
64
65
- Ghosh, S. S., Tourville, J. A., & Guenther, F. H. (2008). A neuroimaging study of premotor lateralization and cerebellar involvement in the production of phonemes and syllables. *Journal of Speech, Language, and Hearing Research*, 51(5), 1183-1202.
- Harrington, A., & Hammond-Tooke, G. D. (2015). Theta Burst Stimulation of the Cerebellum Modifies the TMS-Evoked N100 Potential, a Marker of GABA Inhibition. *PLoS one*, 10(11), e0141284.
- Hartsuiker, R. J., Corley, M., & Martensen, H. (2005). The lexical bias effect is modulated by context, but the standard monitoring account doesn't fly: Related reply to Baars et al.(1975). *Journal of Memory and Language*, 52(1), 58-70.
- Hartsuiker, R. J. (2013). Are forward models enough to explain self-monitoring? Insights from patients and eye movements. *Behavioral and Brain Sciences*, 36(04), 357-358.
- Hassid, E. I. (1995). A case of language dysfunction associated with cerebellar infarction. *Neurorehabilitation and Neural Repair*, 9(3), 157-160.
- Heinks-Maldonado, T. H., Mathalon, D. H., Gray, M., & Ford, J. M. (2005). Fine-tuning of auditory cortex during speech production. *Psychophysiology*, 42(2), 180-190.
- Hickok, G. (2012). Computational neuroanatomy of speech production. *Nature Reviews Neuroscience*, 13(2), 135-145.
- Hokkanen, L. S. K., Kauranen, V., Roine, R. O., Salonen, O., & Kotila, M. (2006). Subtle cognitive deficits after cerebellar infarcts. *European Journal of Neurology*, 13(2), 161-170.
- Houde, J. F., Nagarajan, S., Sekihara, K., & Merzenich, M. M. (2002). Modulation of the auditory cortex during speech: an MEG study. *Journal of Cognitive Neuroscience*, - 14(8), 1125-1138.

1 Imamizu, H., Miyauchi, S., Tamada, T., Sasaki, Y., Takino, R., Pütz, B., Yoshioka, T. &

2 Kawato, M. (2000). Human cerebellar activity reflecting an acquired internal

3 model of a new tool. *Nature*, 403(6766), 192-195.

4
5
6
7 Ito, M. (2008). Control of mental activities by internal models in the cerebellum.

8
9
10 *Nature Reviews Neuroscience*, 9(4), 304-313.

11
12 Jaeger, T. F. (2008). Categorical data analysis: Away from ANOVAs (transformation or

13 not) and towards logit mixed models. *Journal of Memory and Language*, 59(4),

14
15
16
17 434-446.

18
19
20 Jeannerod, M. (1988). *The neural and behavioural organization of goal-directed*

21
22
23 *movements*. Clarendon Press/Oxford University Press.

24
25
26
27
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31
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the hindbrain contribute to the forebrain?. *Behavioral Neuroscience*, 103(5), 998.

Lesage, E., Morgan, B. E., Olson, A. C., Meyer, A. S., & Miall, R. C. (2012). Cerebellar rTMS

disrupts predictive language processing. *Current Biology*, 22(18), R794-R795.

Mariën, P., Engelborghs, S., Fabbro, F., & De Deyn, P. P. (2001). The lateralized

linguistic cerebellum: a review and a new hypothesis. *Brain and Language*, 79(3),

580-600.

Mariën, P., & Manto, M. (Eds.). (2015). *The Linguistic Cerebellum*. Academic Press.

Medina, J. F., & Mauk, M. D. (2000). Computer simulation of cerebellar information

processing. *Nature Neuroscience*, 3, 1205-1211.

McCloskey, D. I. (1981). Corollary discharges: motor commands and perception.

Comprehensive Physiology.

Miall, R. C., & King, D. (2008). State estimation in the cerebellum. *The Cerebellum*, 7(4),

572-576.

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65
- Murdoch, B. E., & Whelan, B. M. (2007). Language disorders subsequent to left cerebellar lesions: a case for bilateral cerebellar involvement in language?. *Folia Phoniatrica et Logopaedica*, 59(4), 184-189.
- Murdoch, B. E. (2010). The cerebellum and language: historical perspective and review. *Cortex*, 46(7), 858-868.
- Nooteboom, S. G.. (2005). Lexical bias revisited: Detecting, rejecting and repairing speech errors in inner speech. *Speech Communication*, 47(1), 43-58.
- Nyffeler, T., Wurtz, P., Lüscher, H. R., Hess, C. W., Senn, W., Pflugshaupt, T., ... & Müri, R. M. (2006). Repetitive TMS over the human oculomotor cortex: comparison of 1-Hz and theta burst stimulation. *Neuroscience Letters*, 409(1), 57-60.
- Petacchi, A., Laird, A. R., Fox, P. T., & Bower, J. M. (2005). Cerebellum and auditory function: An ALE meta-analysis of functional neuroimaging studies. *Human Brain Mapping*, 25(1), 118-128.
- Pickering, M. J., & Garrod, S. (2013). An integrated theory of language production and comprehension. *Behavioral and Brain Sciences*, 36(04), 329-347.
- Pickering, M. J., & Garrod, S. (2014). Self-, other-, and joint monitoring using forward models. *Frontiers in Human Neuroscience*, 8(132).
- Protopapas, A. (2007). Check Vocal: A program to facilitate checking the accuracy and response time of vocal responses from DMDX. *Behavior Research Methods*, 39(4), 859-862.
- Pulvermüller, F., & Fadiga, L. (2010). Active perception: sensorimotor circuits as a cortical basis for language. *Nature Reviews Neuroscience*, 11(5), 351-360.
- Riva, D., & Giorgi, C. (2000). The cerebellum contributes to higher functions during development. *Brain*, 123(5), 1051-1061.

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65
- Schlerf, J., Wiestler, T., Verstynen, T., & Diedrichsen, J. (2014). Big challenges from the little brain—imaging the cerebellum. *Advanced Brain Neuroimaging Topics in Health and Disease—Methods and Applications*.
- Scott, R. B., Stoodley, C. J., Anslow, P., Paul, C., Stein, J. F., Sugden, E. M., & Mitchell, C. D. (2001). Lateralized cognitive deficits in children following cerebellar lesions. *Developmental Medicine & Child Neurology*, *43*(10), 685-691.
- Silveri, M. C., Leggio, M. G., & Molinari, M. (1994). The cerebellum contributes to linguistic production A case of agrammatic speech following a right cerebellar lesion. *Neurology*, *44*(11), 2047-2047.
- Stoodley, C. J., & Schmahmann, J. D. (2009). Functional topography in the human cerebellum: a meta-analysis of neuroimaging studies. *Neuroimage*, *44*(2), 489-501.
- Stoodley, C. J., & Schmahmann, J. D. (2010). Evidence for topographic organization in the cerebellum of motor control versus cognitive and affective processing. *Cortex*, *46*(7), 831-844.
- Strijkers, K., Runnqvist, E., Costa, A., & Holcomb, P. (2013). The poor helping the rich: how can incomplete representations monitor complete ones?. *Behavioral and Brain Sciences*, *36*(04), 374-375.
- Théoret, H., Haque, J., & Pascual-Leone, A. (2001). Increased variability of paced finger tapping accuracy following repetitive magnetic stimulation of the cerebellum in humans. *Neuroscience Letters*, *306*(1), 29-32.
- Urban, P. P., Marx, J., Hunsche, S., Gawehn, J., Vucurevic, G., Wicht, S., ... & Hopf, H. C. (2003). Cerebellar speech representation: lesion topography in dysarthria as derived from cerebellar ischemia and functional magnetic resonance imaging. *Archives of Neurology*, *60*(7), 965-972.

1 Wolpert, D. M., Ghahramani, Z., & Jordan, M. I. (1995). An internal model for
2 sensorimotor integration. *Science-AAAS-Weekly Paper Edition*, 269(5232), 1880-
3
4 1882.
5
6

7 Zettin, M., Cappa, S. F., D'amico, A., Rago, R., Perino, C., Perani, D., & Fazio, F. (1997).
8
9 Agrammatic speech production after a right cerebellar
10
11 haemorrhage. *Neurocase*, 3(5), 375-380.
12
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The Cerebellum and Self-monitoring in Language Production

Appendix A.

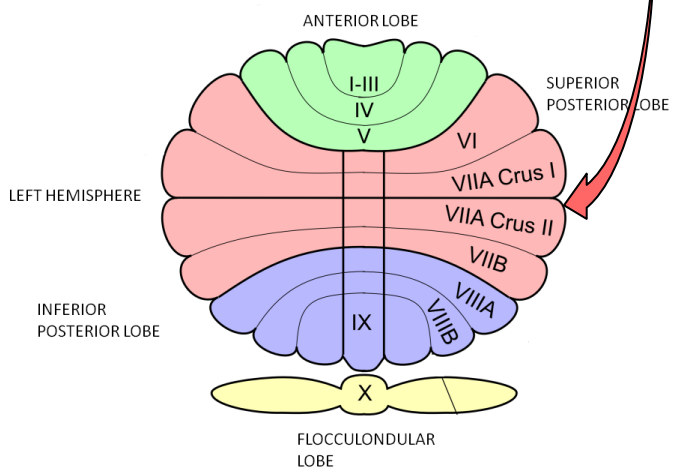
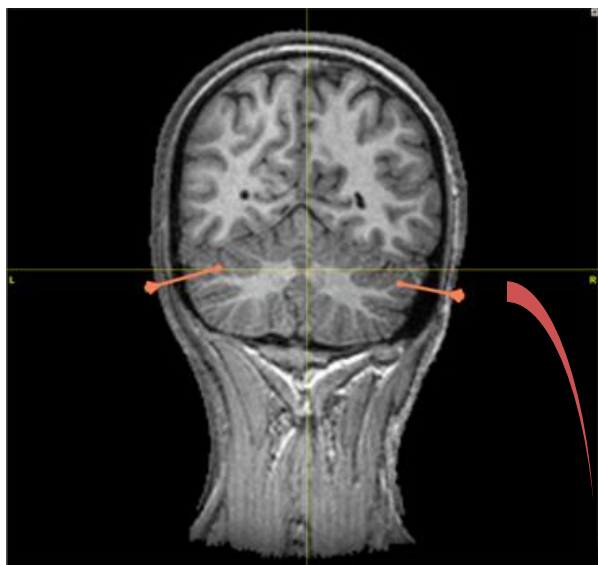
	LEXICAL				NON-LEXICAL			
	Set A		Set B		Set A		Set B	
1								
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4	malade	sinus	durée	pédale	légion	barreau	bouton	coussin
5	dentier	répit	raison	maquette	ciment	belote	loto	jonction
6	faveur	semelle	ragot	fumeur	poker	sapin	primeur	colosse
7	tendue	voiture	marine	fission	musée	peinture	fournée	bordée
8	rosier	gâteau	coteau	poupon	lavoir	moisson	boulette	jointure
9	matin	passage	tonus	boucan	monteur	filleul	poulet	taverne
10	pillage	sommier	lutin	bocal	tracas	recteur	couture	poison
11	cadeau	rocher	garage	palette	cuisson	manière	têtard	lamelle
12	verger	bison	nature	ration	gardon	façon	croupier	filon
13	ministre	seringue	crochet	briquet	tonton	rouleau	paresse	fraction
14	titre	voile	clé	bol	vieux	brique	mâche	pomme
15	ciel	fil	gag	troupe	robe	coeur	lueur	cote
16	lierre	poupe	foire	prime	masque	fosse	plaque	gerbe
17	flic	coin	douche	salle	veste	singe	place	fable
18	butte	lave	gaule	tare	boule	lampe	four	dague
19	dame	rose	banque	marque	roc	panne	braise	contre
20	serre	valve	natte	pièce	course	forge	grange	touche
21	mec	bise	note	puits	vase	pion	liège	tête
22	rage	cap	dune	lieu	selle	fiche	suite	disque
23	casse	tube	soir	lac	soupe	foudre	cause	gousse
24	gosier	râteau	blé	col	lecteur	joker	toison	boulet
25	patin	massage	loir	sac	lanière	fêtard	gamelle	ponton
26	sillage	pommier	mise	bec	maçon	journée	pilon	bouture
27	radeau	cocher	rap	cage	bouleau	moto	traction	piment
28	berger	vison	tag	groupe	poussin	savoir	carreau	roulette
29	sinistre	meringue	vitre	toile	fonction	troupier	pelote	fracas
30	saveur	femelle	verre	salve	molosse	lardon	lapin	fusée
31	fagot	rumeur	poire	frime	cordée	frimeur	ceinture	région
32	farine	mission	souche	dalle	pointure	conteur	boisson	caresse
33	poteau	coupon	gare	taule	caverne	mouton	tilleul	buisson
34	cil	fiel	salade	minus	pelle	risque	crique	pousse
35	pierre	loupe	rentier	dépit	case	sueur	coupe	frange
36	foin	clic	maison	raquette	verbe	tour	bosse	montre
37	lutte	bave	venue	toiture	sable	poudre	linge	bourse
38	rame	dose	purée	dédale	vague	foule	rampe	soeur
39	barque	manque	bonus	toucan	pause	mouche	casque	fraise
40	patte	nièce	butin	local	tâche	piège	gorge	canne
41	pote	nuits	parage	galette	fête	lobe	lion	vote
42	lune	dieu	rature	nation	doc	geste	biche	dieux
43	tasse	cube	brochet	criquet	glace	fuite	flaque	somme
44	cause	panne	selle	pomme	clé	pièce	butte	cap
45	soupe	coeur	vase	cote	ciel	tare	mec	lave

The Cerebellum and Self-monitoring in Language Production

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

Figure 1

A



B

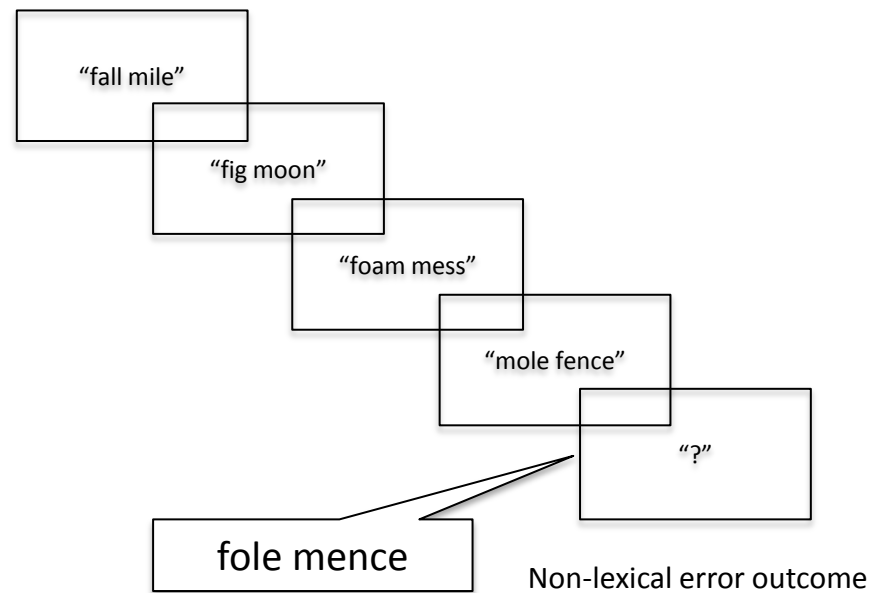
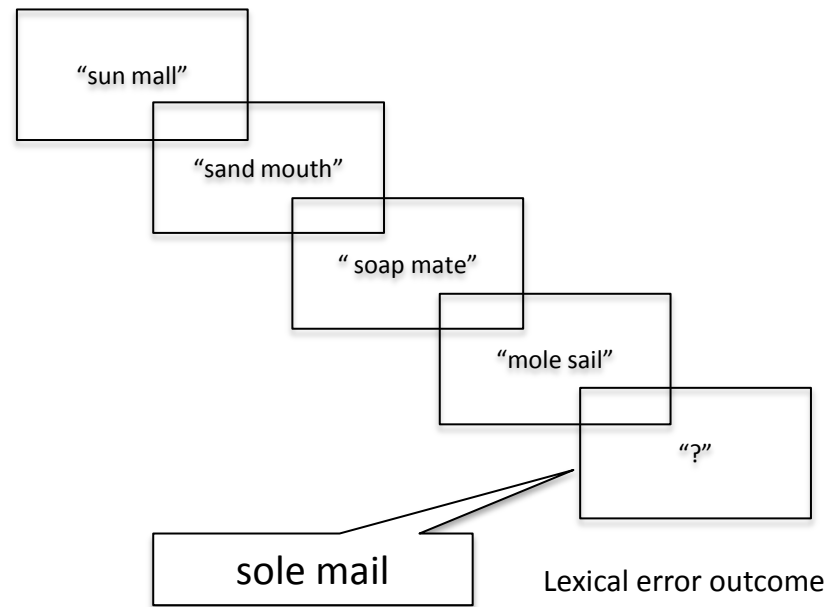
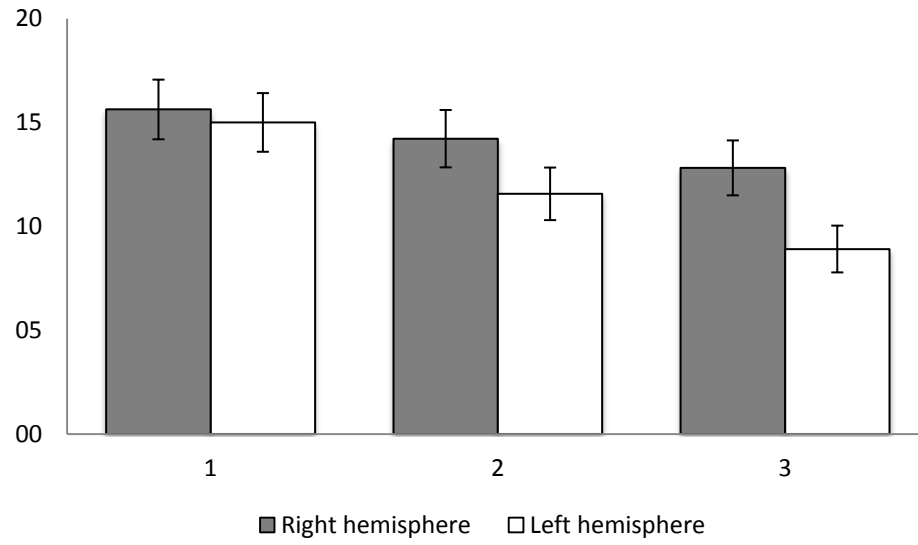


Figure 1. Schematic representation of the stimulation sites and the experimental task.

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



B

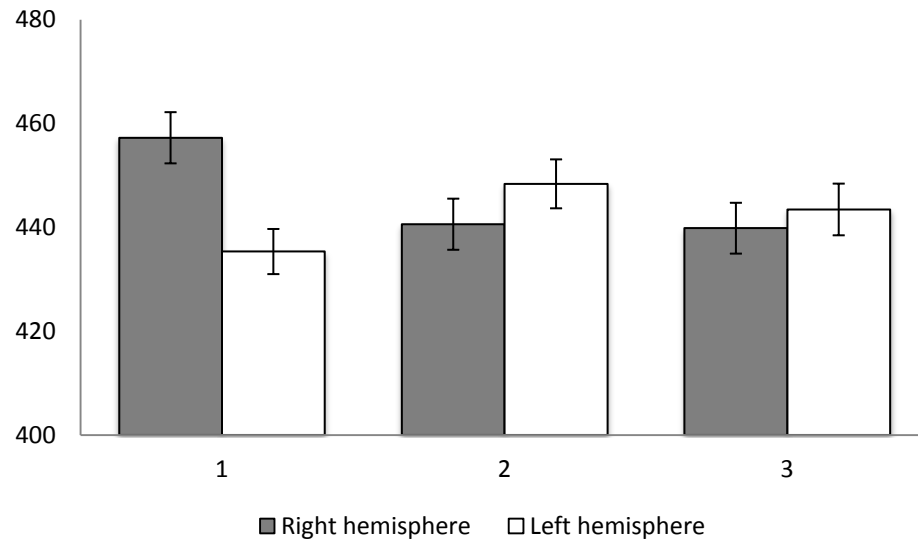


Figure 2. Error-rates and Response times

(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.