



The cerebellum, internal models and prediction in ‘non-motor’ aspects of language: A critical review



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ARTICLE INFO

Article history:

Received 12 December 2014

Revised 25 July 2015

Accepted 6 August 2015

Available online 28 August 2015

Keywords:

Language

Prediction

Cerebellum

Internal models

Associative learning

Priming

Default-mode network

ABSTRACT

The emergence of studies on cerebellar contributions in ‘non-motor’ aspects of predictive language processing has long been awaited by researchers investigating the neural foundations of language and cognition. Despite (i) progress in research implicating the cerebellum in language processing, (ii) the widely-accepted nature of the uniform, multi-modal computation that the cerebellum implements in the form of internal models, as well as (iii) the long tradition of psycholinguistic studies addressing prediction mechanisms, research directly addressing cerebellar contributions to ‘non-motor’ predictive language processing has only surfaced in the last five years. This paper provides the first review of this novel field, along with a critical assessment of the studies conducted so far. While encouraging, the evidence for cerebellar involvement in ‘non-motor’ aspects of predictive language processing remains inconclusive under further scrutiny. Future directions are finally discussed with respect to outstanding questions in this novel field of research.

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1. Introduction

The cerebellum was traditionally seen as exclusively supporting the coordination of skilled, voluntary movement, gait, posture, balance, control of muscle tone, motor learning and articulation, with such involvement being reported for two centuries now. Readers are referred to [Dow and Moruzzi \(1958\)](#) for a thorough review of 19th century studies in the field, and to [Manto et al. \(2012\)](#) for a recent account. Over the last few decades, however, especially after the seminal work by the Leiners (see [Leiner \(2010\)](#) for a brief review), cumulative evidence has supported cerebellar involvement in a wide range of higher cognitive functions, e.g. memory, executive functions, visuospatial processing, emotional regulation, thought modulation, and, crucially, language ([Mariën et al., 2014](#)). In parallel, it has become increasingly clear that the cerebellum communicates in segregated anatomical loops with motor and pre-frontal cortex ([Strick, Dum, & Fiez, 2009](#)). Its cytoarchitectural uniformity supports the idea that its computations for motor control should guide hypotheses about its contributions in higher cognitive processes ([Ramnani, 2006](#)), including language ([Ito, 2000a, 2008](#)). However, research of relevance has, until very recently, been predominantly conducted in three poorly interfacing fields: (i) work on cerebellar internal models in motor and non-motor aspects of behavior, without addressing their contribution in

language; (ii) research on cerebellar involvement in non-motor aspects of language processing, with no computational grounding; (iii) studies conceptualizing predictive operations in language processing in terms of outputs of internal models, without addressing cerebellar circuitry as the most likely candidate for their implementation. This review will focus on studies of cerebellar involvement in the generation of semantic and phonological predictions above the lexical level in language comprehension. The interaction of predictive processes at different levels and the covert employment of language production mechanisms in comprehension ([Pickering & Garrod, 2007](#)) remain beyond the scope of this review.

2. ‘Cerebellum’ and ‘Prediction’, but no ‘Language’

The contributions of the cerebellum in the automation of motor control have been well studied, and are consistent with the view that learning mechanisms store ‘motor memory’ through the diminishing synaptic efficacy between cerebellar neurons and their inputs ([Albus, 1971; Marr, 1969](#)). Control theoretic accounts suggest that such mechanisms allow cerebellar circuitry to acquire internal models that ultimately implement in an automatic fashion the movement-related processes initially established in the motor cortex ([Ito, 1970, 1984; Ramnani, 2006; Wolpert, Miall, & Kawato, 1998](#)). For instance, an internal (‘forward’) model of the arm’s dynamics, receives, as input, information on the current position and velocity of the arm, along with an ‘efference copy’ of motor

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commands issued by the central nervous system, and outputs a prediction of the future position and velocity of the arm. Because of conduction delays in efferent and afferent pathways, the central nervous system is not immediately updated on changes in the peripheral motor system, and any recent commands issued may be yet to affect the musculature. Internal models are employed more rapidly, providing information about future properties of the controlled object, a fortiori in cases where accurate sensory feedback may be totally absent. This internal model 'feedback' allows the perceiver to rapidly interpret the perceptual signal and react accordingly, complete percepts received incompletely and/or under noise, and disambiguate in situations of uncertainty (Jordan & Wolpert, 2000). While internal models are conceivably located in all brain regions with synaptic plasticity that receive and send relevant information for their input and output (Kawato, 1999), a broad range of electrophysiological (Gilbert & Thach, 1977; Medina & Lisberger, 2009), imaging (Blakemore, Frith, & Wolpert, 2001; Desmurget et al., 2001; Imamizu et al., 2000; Puttemans, Wenderoth, & Swinnen, 2005), and clinical studies (Müller & Dichgans, 1994; Nowak, Timmann, & Hermsdörfer, 2007) have established the cerebellum as 'the most likely site for forward models to be stored' (Kawato et al., 2003, p. 171).

However, the cerebellum exhibits a combination of two striking properties that support the involvement of its internal models beyond motor control: namely, its 'essentially uniform, monotonously repetitive architecture' (Schmahmann, 2000, p. 206) and its massive connectivity with virtually all major subdivisions of the brain. In particular, axonal fiber-tracing studies have identified projections from a broad range of neocortical areas to the pontocerebellar system, and even further to specific cerebellar lobules. These lobules return projections to the very same cerebral cortical areas via the cerebellar nuclei and thalamus, hence operating by means of segregated anatomical loops. Characteristically, the primary motor cortex selectively communicates with cerebellar lobules HV, HVI, HVIIb, and HVIIIa (Kelly & Strick, 2003; Middleton & Strick, 2000). Importantly, though, a substantial range of prefrontal areas send inputs to the pontine nuclei, which, along with the inferior olive, form the two major sources of input to the cerebellum. These prefrontal areas span from area 10 through to posterior regions of area 8, crucially including area 45B in the rostral bank of the inferior limb of the arcuate sulcus (Schmahmann & Pandya, 1997). Prefrontal neurons provide inputs to Purkinje cells in lobule VIIa and Crura I and II in lobule HVIIa (Kelly & Strick, 2003). This has encouraged the idea that '[i]f closed-loop circuits reflect a general rule, then all of the areas of cerebral cortex that project to the cerebellum are the target of cerebellar output' (Strick et al., 2009, p. 422). Furthermore, lobule HVIIa boasts unparalleled computational power: it comprises nearly 50% of the cerebellar volume (Balsters et al., 2010), while the human cerebellum itself contains more neurons than all the rest of the nervous system (see Leiner (2010) for references). Moreover, recent work employing intrinsic functional connectivity in humans has demonstrated that HVIIa Crus I/II can be further subdivided on the basis of functional connectivity with anterior, ventromedial, and dorsolateral regions in the prefrontal cortex (Buckner, Krienen, Castellanos, Diaz, & Yeo, 2011; Krienen & Buckner, 2009). Since the uniformity of cellular organization across the cerebellar cortex implies identity in the computations performed (e.g. Bloedel, 1992; Schmahmann & Pandya, 1997), the same forms of plasticity might support the automation of cognitive processes, and knowledge on cerebellar motor learning has indeed started to guide the study of cerebellar contributions to cognition (Ramnani, 2006; Fig. 1).

Associative learning represents a fundamental mechanism by which cerebellar internal models are seen to work. Classical conditioning, for instance, provides the most basic form of associative memory formation, and the cerebellum has long been established

as a fundamental site (e.g. Christian & Thompson, 2005; Thompson et al., 1997) in both comparative (e.g. McCormick & Thompson, 1984) and human clinical studies (e.g. Daum et al., 1993; Timmann et al., 1996). Crucially, the cerebellum is involved in non-motor aspects of associative learning. In a series of studies, cerebellar patients acquired associations between colors and numerals by trial-and-error. In comparison with normal controls, patients were significantly slower in learning the correct associations, and were impaired in recognizing them later. Control conditions established that this learning deficit could not be reduced to patients' motor impairment (Drepper, Timmann, Kolb, & Diener, 1999; Timmann et al., 2002, 2004). Moreover, recent fMRI work has shown that HVIIa Crura I/II are involved in the acquisition and employment of first- and second-order rules. In these studies, subjects acquired arbitrary associations by trial-and-error of visual stimuli with manual responses (first-order rules) or with instructions on the selection of a first-order rule (second-order rules). With the employment of delayed response tasks, activity time-locked to the onset of the rule-related cue was disambiguated from that for motor responses or visual feedback (Balsters & Ramnani, 2008, 2011; Balsters, Whelan, Robertson, & Ramnani, 2013). These findings corroborate early proposals that the cerebellum 'predicts' and 'prepares' the internal conditions required for sensory, motor, autonomic, memory-related, attention-related, affective, or linguistic operations, by acquiring the 'predictive relationships among temporally ordered multidimensional sequences of exogenously derived [...] and endogenously derived [...] neural activities' (Courchesne & Allen, 1997, p. 2). More recently, contributions of cerebellar internal models to multi-modal associative learning have been thoroughly examined in two reviews (Bellebaum & Daum, 2011; Timmann et al., 2010). Quite importantly, though, neither of those discusses the ways in which cerebellar internal models could contribute to non-motor aspects of linguistic associative learning and processing.

3. 'Cerebellum and Language', but no 'Prediction'

In parallel, studies on the cerebellar contributions in language have started to flourish over the last few decades. Although still often marginalized in neurobiological models of language processing (e.g. Friederici, 2012; Hickok & Poeppel, 2007), the 'ongoing enigma' of the linguistic cerebellum has been attracting significant attention (Mariën et al., 2014). Indeed, there has been accumulating clinical evidence for even a 'lateralized linguistic cerebellum' (Mariën, Engelborghs, Fabbro, & De Deyn, 2001), and meta-analyses of imaging studies locate activations related to language processing in right hemispheric cerebellar regions (Chen, Ho, & Desmond, 2014; Stoodley & Schmahmann, 2009). For an up-to-date account of the evidence, the reader is encouraged to consult De Smet, Paquier, Verhoeven, and Mariën (2013), as well as papers in this special issue. Even so, such discussion has not incorporated the way in which cerebellar internal models may be involved in language processing, until very recently.

4. 'Language and Prediction', but no 'Cerebellum'

Turning to prediction mechanisms in language processing, these are anything but novel a concept in studies of psycholinguistics and the neurobiology of language. For decades now, research has shown that predictions at the sentence level modulate speech perception and production (Lieberman, 1963) and accelerate syntactic processing (e.g. Staub & Clifton, 2006; see also discussion in Sturt & Lombardo, 2005).

Unsurprisingly, then, prediction in language processing is often conceptualized to operate in the form of internal model outputs.

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