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Embodied cognition and the cerebellum: Perspectives from the Dysmetria of Thought and the Universal Cerebellar Transform theories

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ABSTRACT

In this report, we analyze the relationship between embodied cognition and current theories of the cerebellum, particularly the Dysmetria of Thought theory and the concept of the Universal Cerebellar Transform (UCT). First, we describe the UCT and the Dysmetria of Thought theories, highlight evidence supporting these hypotheses and discuss their mechanisms, functions and relevance. We then propose the following relationships. (i) The UCT strengthens embodied cognition because it provides an example of embodiment where the nature and intensity of the dependence between cognitive, affective and sensorimotor processes are defined. (ii) Conversely, embodied cognition bolsters the UCT theory because it contextualizes a cerebellum-focused theory within a general neurological theory. (iii) Embodied cognition supports the extension to other brain regions of the principles of organization of cerebral cortical connections that underlie the UCT: The notion that cytoarchitectonically determined transforms manifest via connectivity as sensorimotor, cognitive and affective functions resonates with the embodiment thesis that cognitive, affective and sensorimotor systems are interdependent. (iv) Embodied cognition might shape future definitions of the UCT because embodiment redefines the relationship between the neurological systems modulated by the UCT. We conclude by analyzing the relationship between our hypotheses and the concept of syntax and action semantics deficits in motor diseases.

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1. Introduction

1.1. Embodied cognition

The embodied cognition research program (Shapiro, 2007, 2011) (hereafter, embodied cognition) reconfigures the nature of cognition by regarding the body and the environment as significant factors in the way we think and feel. This line of inquiry explores the extent to which "*aspects of the agent's body beyond the brain play a significant causal or physically constitutive role in cognitive processing*" (Wilson & Foglia, 2016). It includes the study of the relationship between sensorimotor, cognitive and affective neurological systems. The notion of embodied cognition emerged from a wide diversity of empirical observations and theoretical reflections, from Heidegger's analysis of being-in-the-world (Heidegger, 1962) to behavioral and functional neuroimaging experiments (e.g., Hauk, Johnsrude, & Pulvermüller, 2004). In the present analysis, we develop the hypothesis that there is a strong mutual interaction between the fields of embodied cognition and the cognitive neuroscience of the cerebellum. Specifically, we focus on the relationship between sensorimotor, cognitive and affective neurological systems inherent in embodied cognition (see Wilson, 2002; "Off-Line Cognition Is Body Based") and two fundamental theoretical underpinnings of cerebellar cognition – Dysmetria of Thought and the Universal Cerebellar Transform (UCT).

Studies exploring the role of sensorimotor systems in cognition and emotion support the notion that action cognition is grounded in the sensorimotor system. Understanding sensorimotor concepts activates sensorimotor cortices (Hauk et al., 2004; Tettamanti et al., 2005); listening to action sentences related to the hand or foot results in slower response times and decreased amplitude of motor evoked potentials recorded from the muscles of the hand and foot (Buccino et al., 2005); and lesions of sensorimotor cortices impair action-related linguistic abilities (Kemmerer, Rudrauf, Manzel, & Tranel, 2012). The formation of abstract concepts unrelated to action cognition seems also to be influenced by sensorimotor processes. Squeezing a hard ball increases the chance of judging sex-ambiguous faces as male (Slepian, Weisbuch, Rule, & Ambady, 2011); hand sanitizer was preferred after lying in an e-mail (Lee & Schwarz, 2010); holding hot coffee makes it more likely that one will judge a person as having a warmer personality and holding a hot therapeutic pad increases the likelihood of choosing a gift for a friend instead of for oneself (Williams & Bargh, 2008); and individuals judge an issue as more important when holding a heavy clipboard (Jostmann, Lakens, & Schubert, 2009; see, however, an ongoing discussion regarding the replicability of some of these findings [Rabelo, Keller, Pilati, & Wicherts, 2015], but also other studies reporting the influence of similar bodily sensations on a variety of abstract judgments [e.g., Schneider, Parzuchowski, Wojciszke, Scharz, & Koole, 2015; Chandler, Reinhard, & Schwarz, 2012; Ackerman, Nocera, & Bargh, 2010]). Even everyday use of language seems to reflect a close relationship between sensorimotor principles and cognitive schemas. This is exemplified by statements such as "*I have control over him*", or "*He is under my control*", as argued in Lakoff's "Metaphors we live by" (Lakoff & Johnson, 1980).

1.2. Theories of cerebellar function: Dysmetria of Thought and the Universal Cerebellar Transform (UCT)

Anatomical, clinical and neuroimaging findings suggest that the cerebellum is engaged not only in motor control but also in cognitive and affective functions (Baillieux, De Smet, Paquier, De Deyn, & Mariën, 2008; E, Chen, Ho, & Desmond, 2014; Middleton & Strick, 1994; Schmahmann & Pandya, 1989; Schmahmann, 1991, 1996; Schmahmann & Sherman, 1998; Stoodley & Schmahmann, 2009; Stoodley, Valera, & Schmahmann, 2012; see also; Koziol et al., 2014; Ramnani, 2006; Schmahmann, 1997; Schmahmann, 2004; Sokolov, Miall, & Ivry, 2017). Although it has been argued that there are only minor connections between the cerebellum and cognitive areas of the cerebral cortex, that imaging evidence may be confounded by eye movements, and that cognitive deficits in cerebellar patients may result from damage to other brain structures (Glickstein, 1993; Glickstein & Doron, 2008), the sizeable body of evidence favors a role of the cerebellum in cognition and affect. In this way, the central question in cerebellar neurobiology is no longer whether the cerebellum plays a role in cognition and emotion, but instead *how* the cerebellum participates in these neurological functions. Recent publications highlight that "*the functional participation of cerebellar structures in nonmotor cortical networks remains poorly understood and is highly understudied, despite the fact that the cerebellum possesses many more neurons than the cerebral cortex*" (Brissenden, Levin, Osher, Halko, & Somers, 2016).

The theory of the UCT holds that the same neurological process subserves cerebellar modulation of movement, cognition and emotion. The Dysmetria of Thought theory, predicated on the notion of a UCT, posits that motor, cognitive and affective symptoms in cerebellar patients (the Cerebellar Cognitive Affective Syndrome [CCAS; Levisohn, Cronin-Golomb, & Schmahmann, 2000; Schmahmann & Sherman, 1998] or Schmahmann's syndrome [Manto & Mariën, 2015]) are consequences of a singular neurological dysfunction, the Universal Cerebellar Impairment. This manifests in the motor domain as dysmetria of movement (Holmes, 1939), and in the cognitive/affective domains as Dysmetria of Thought (Schmahmann, 1991, 2000, 2010) (Fig. 1).

The study of the UCT can be parsed into the following lines of analysis: (a) Does it exist? (b) What is its underlying mechanism or computation? (c) What is its function?

1.2.1. Is there a UCT?

The existence of a UCT has been supported by the following observations:

(1) Cerebellar cortex cytoarchitecture is essentially constant throughout its structure (Ito, 1993; Voodg and Glickstein, 1998) – as function follows form, this uniform cerebellar anatomy suggests a uniform cerebellar function (Ito, 1993; Ramnani, 2006; Schmahmann, 1991, 2001). A recent review (Cerminara, Lang, Sillitoe, & Apps, 2015) highlighted cerebellar anatomical, physiological, and genetic regional differences which have long been known to exist and argued that, in consequence, "*the concept of a universal cerebellar transform probably does not hold true*". Indeed, cerebellar cortex

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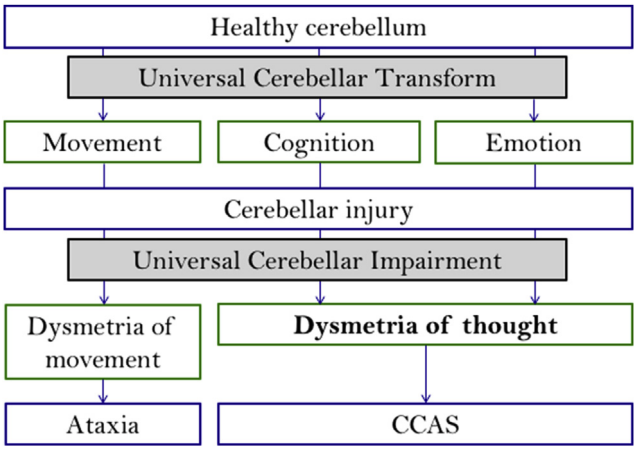

Fig. 1 – Schematic of the Dysmetria of Thought theory (Schmahmann, 1991, 2000, 2010). Adapted from Guell et al., 2015.

cytoarchitecture is not *completely* uniform. The UCT theory has been developed on the observation of an *essentially* (yet not completely) uniform cerebellar cortical structure, contrasting with the heterogeneous cerebral cortical cytoarchitecture (Schmahmann, 2000: "*Whereas immunohistochemistry has identified that cerebellar cortex contains anatomically identifiable parasagittal bands that appear to have connectional and physiologic specificity, there are no "Brodmann areas" in the cerebellum… The histology suggests that the transformations performed by the cerebellum are invariant throughout the structure.*"). Other authors have argued similarly, e.g., "*although there is some variation across the cortex, this is minor in relation to the scale of uniformity*" (Ramnani, 2006).

(2) Cognitive and affective problems follow the logic of motor symptoms in patients with cerebellar injury – this common pattern of deficits is expected after the disruption of a common neurological process. Cerebellar damage impairs the rate, rhythm and accuracy of limb trajectories, but motor strength and power remain preserved. Similarly, damage to the cerebellum disrupts metalinguistic abilities, e.g., the ability to understand metaphorical expressions or to construct sentences with pragmatic quality, more than the basic structures of grammar and semantics. We showed this pattern of language deficits (Guell, Hoche, & Schmahmann, 2015) in a study in which the Oral Sentence Production Test, a constrained language task that examines basic semantic and syntactic abilities (Caplan & Hanna, 1998), revealed no deficits in patients with cerebellar injury. In contrast, the same patients had impaired performance on the Test of Language Competence – Expanded (Wiig & Secord, 1989), a test that examines metalinguistic abilities including the ability to identify alternative meanings of lexical and structural ambiguities, make logical inferences in short paragraphs, construct sentences with correct grammatical and pragmatic quality for a given context, and understand metaphorical expressions. Whereas cerebral cortical damage may result in loss of a function such as aphasia and paralysis, cerebellar damage degrades the precision, efficiency or coordination of that function as manifested in metalinguistic deficits or motor ataxia. Similarly, impairment in judging facial emotional expressions in cerebellar patients is understood as a deficit in a rapid, automatic and implicit processing of facial expressions (Hoche, Guell, Sherman, Vangel, & Schmahmann, 2016); and neuropsychiatric manifestations in cerebellar patients are conceptualized as an impairment in the implicit, automatic modulation of emotions (Schmahmann, Weilburg, & Sherman, 2007).

(3) Theta burst stimulation to two different cerebellar regions results in similar increases in the complexity and variability of brain signals across multiple time scales, i.e., multiscale entropy, in two different cerebral cortical regions (Farzan, Pascual-leone, Schmahmann, & Halko, 2016). This common pattern of electrophysiological changes is expected after the stimulation of a common neurological process.

(4) A precise connectivity map observed in tract tracing (see Schmahmann & Pandya, 1997, 2008; for a review; Dum & Strick, 2003), resting-state functional connectivity (Buckner, Krienen, Castellanos, Diaz, & Yeo, 2011; Habas et al., 2009; O'Reilly, Beckmann, Tomassini, Ramnani, & Johansen-berg, 2010), and tractography studies (Granziera et al., 2009) links the cerebellum with multiple distinct sensorimotor, association and paralimbic areas of the cerebrum and allows a topographically specific cerebellar modulation of cerebral activity (Halko, Farzan, Eldaief, Schmahmann, & Pascual-leone, 2014). The notion of a singular neurological computation in the cerebellum might appear at odds with the remarkable diversity of cerebellar functions from movement coordination to cognition and emotion, and the presence of multiple distinct functional cerebellar subregions (E et al., 2014; Stoodley & Schmahmann, 2009; Stoodley et al., 2012). This apparent paradox is solved, however, by recognition of the connectional specificity of the cerebrocerebellar pathways which explains how functional topography and behavioral heterogeneity can emerge from a constant neurological process, the UCT.

1.2.2. *What is the mechanism of the UCT?*

Here we consider "function" to be the neurobehavioral outcome/consequence of a neural mechanism. In this view, a function may be inferred from behavioral observations. In contrast, we will consider "mechanism" to be the process by which a node in a distributed neural circuit performs its computation/transform necessary for the integrity of the network as a whole. Therefore, a mechanism may be ascertained from observations at multiple levels, including cellular physiology, neuroimaging, computational models, neuropsychological assessments, and clinical observations.

The original description of the concept of the UCT hypothesizes that the cerebellum performs its functions by acting as an *oscillation dampener*, rapidly and automatically optimizing performance according to context (Schmahmann, 1996). The definition is derived from the

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motor system and by analogy applies equally to the modulation of intellect and emotional processing. It is supported by behavioral observations: impairment in judging facial emotional expressions in cerebellar patients is understood as deficits in rapid, automatic and implicit processing of facial expressions (Hoche et al., 2016); metalinguistic deficits in cerebellar patients are conceptualized as disruptions in automatic adjustment of grammatical and semantic abilities to a linguistic context (Guell et al., 2015); and neuropsychiatric manifestations in cerebellar patients are viewed as an exaggeration (overshoot) or diminution (undershoot) of responses to the internal or external environment and as impairment in the implicit, automatic modulation of emotions (Schmahmann et al., 2007).

Additional investigations addressing the putative mechanisms underlying cerebellar functions have generated multiple (not mutually exclusive) hypotheses applicable to both motor and nonmotor domains, and these are compatible with the original concept of the UCT. These hypotheses include *prediction* (Miall, Christensen, Cain, & Stanley, 2007; Lesage, Morgan, Olson, Meyer, & Miall, 2012), *event-timing* (Ivry & Keele, 1989; Ivry, Spencer, Zelaznik, & Diedrichsen, 2002), *error-driven adjustment* (Ben-Yehudah, Guediche, & Fiez, 2007), *sequencing* (Molinari, Chiricozzi, Clausi, & Tedesco, 2008), *control of temporal dynamics* (Farzan et al., 2016), and *generation of internal models* (Balsters & Ramnani, 2011; Ito, 2008). The latter holds that the cerebellum generates, and updates according to error-driven adjustment, internal models that mimic and predict motor and nonmotor behavior. These models influence the cerebral control of motor and nonmotor behavior (forward model), or directly manipulate the final outputs of sensorimotor, cognitive and affective functions (inverse models) (see Ito, 2008; Ishikawa, Tomatsu, Izawa, & Kakei, 2016; Ramnani, 2006 for a discussion on forward *vs* inverse models and their supporting evidence). The internal models hypothesis largely overlaps with studies supporting a role of the cerebellum in prediction, timing, sequencing, and error-driven adjustment (as reviewed in Sokolov et al., 2017). These hypotheses are derived from observations at multiple levels, including cellular physiology, cytoarchitecture and cerebrocerebellar interactions (e.g., Ito, 2008; Schmahmann, 1996), neuroimaging (e.g., Balsters & Ramnani, 2011), computational models (e.g., Wolpert, Miall, & Kawato, 1998), electroencephalography and theta burst transcranial magnetic stimulation (Farzan et al., 2016), as well as neuropsychological assessments of the CCAS (Molinari et al., 2008; Schmahmann & Sherman, 1998), including modifications in behavior resulting from theta burst stimulation (Del Olmo et al., 2007).

1.2.3. *What is the function of the UCT?*

The theory of the UCT holds that a singular mechanism emerges from an essentially uniform cerebellar anatomy, and performs its computation on different channels of information processing subserved by anatomically precise connections linking focal cerebellar regions with different cerebral areas. This enables the UCT to manifest as different functions, from movement coordination to cognition and emotion. In this view, different functions of the UCT (inferred from behavioral observations and guided by motor analogies, e.g., the regulation of rate, rhythm and accuracy of movement, and therefore the regulation of speed, capacity, consistence and appropriateness of emotions [Schmahmann, 1991]) would be understood as different manifestations of the common mechanism.

Examples abound in nature by which a common mechanism performs multiple functions depending on its environment or location. Cells use polypeptides in different ways by locating them in different environments. This is exemplified by the functions of the enzyme glyceraldehyde-3-phosphate dehydrogenase which include DNA repair, tRNA export, membrane fusion and transport, and cytoskeletal dynamics – depending on its location (Sirover, 2011). Language function can also change depending on the environment ("*Think of exclamations, with their completely different functions: "No!"*, or "*Water!*"" [Wittgenstein, 1953]). In the cerebellum, because of its connections with different areas of the cerebral hemispheres, the UCT operates in different environments and therefore manifests as different functions. In this view, regional differences in function resulting from cerebellar modulation (the UCT) emerge from the heterogeneity of its connectivity, i.e., differences in environment/location, rather than from variation in cerebellar cytoarchitecture or physiology.

1.2.4. *What is the relevance of the UCT theory?*

Confirmation of the UCT would guide the definition of the functions of the cerebellum. If cerebellar functions are shown to emerge from a common mechanism (the UCT), cerebellar functions are expected to share common underlying principles. As a consequence, definition of one cerebellar function will guide the definition of other cerebellar functions. Thus, if cerebellar damage impairs the rate, rhythm and accuracy of movement, the logical inference by analogy is that the cerebellum contributes to affect by regulating the speed, capacity, consistence and appropriateness of emotions (Schmahmann, 1991). Additionally, evidence supporting the existence of a UCT would facilitate research into the mechanism of the cerebellum since it would guide future investigations to focus on the description of one single mechanism underlying all cerebellar functions. A recent review article (Sokolov et al., 2017) provides a somewhat analogous argument: "*If principles of information processing are indeed similar across the cerebellum, we should consider mechanistic hypotheses that would be consistent across task domains. Hence, our understanding of cerebellar involvement in cognition may benefit from considering the substantial knowledge we have on how the cerebellum contributes to sensorimotor control*". We would add that, therefore, there is a need for future research to directly test the UCT hypothesis. Accordingly, we would include "Is there a Universal Cerebellar Transform?" as one of the outstanding questions presented in Sokolov et al., 2017.

Better understanding of the mechanism and functions of the cerebellum facilitated by the confirmation of the UCT theory could potentially impact the understanding, diagnosis and treatment of the ataxias as well as other diseases where cerebellar structural and functional abnormalities have been identified; such as major depressive disorder, anxiety disorders, bipolar disorder, schizophrenia, attention deficit and hyperactivity disorder, and autism spectrum disorders (for a review, see Phillips, Hewedi, Eissa, & Moustafa, 2015).

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There is therefore a great need to directly test the UCT hypothesis, as well as to explore its relationship with the next step in the evolution of standard cognitive science (Wheeler, 2005) – embodied cognition. The following sections will provide novel insights into the relationship between embodiment and the UCT theory.

2. The UCT theory strengthens the notion of embodied cognition

The embodiment thesis holds that cognitive and affective functions are not independent from sensorimotor functions (see Section 1.1). Many questions remain. "*Given that we have good reason to think that the body influences cognition in surprisingly robust ways, the central question is no longer whether or not some cognitive processes are embodied. Other questions have come to the forefront. To what extent are cognitive processes embodied? Are there disembodied processes? Among those that are embodied, how are they embodied? Is there more than one kind of embodiment? Is embodiment a matter of degree?*" (Dove, 2015). We suggest that the UCT theory can serve as an example of embodiment which satisfies the conditions listed below, that it provides novel insights into the relationship between sensorimotor, cognitive and affective neurological process, and that it strengthens the notion of embodied cognition.

First, motor and non-motor functions involve distinct neurological processes such as generation, association, and modulation. Which processes of motor and non-motor function does the embodiment thesis make reference to? The UCT provides an example of embodiment where the process analyzed – the cerebellar modulation of movement, thought and emotion – is clearly defined.

Second, the nature of dependence between cognitive, affective and sensorimotor functions could be either causal, i.e., sensorimotor systems *influence* cognitive and affective systems, or constitutive, i.e., sensorimotor systems *are on a continuum with* cognitive and affective systems. What nature of dependence does embodied cognition make reference to? The UCT represents a case of *constitutive* dependence between sensorimotor, cognitive and affective functions. Each cerebellar corticonuclear microcomplex (Ito, 2008) performs the same computation regardless of the nature of the information being processed (Schmahmann, 1991, 2000), and therefore principles of cerebellar cognitive and affective modulation are *constituted by* the same principles of cerebellar modulation of movement.

Third, the intensity of the dependence could range from cognition and emotion being mildly influenced or partially constituted by sensorimotor function, to extremely influenced by or fully constituted (identical) to sensorimotor function. What degree of intensity does the embodiment thesis make reference to? The UCT provides an example of embodiment where the intensity of dependence between sensorimotor, cognitive and affective neurological processes is *maximally* constitutive – the UCT holds that the cerebellar contribution to cognitive and affective neurological processes are essentially *identical* to cerebellar sensorimotor processes.

In summary, the UCT theory provides a case of embodiment that addresses critical questions of embodied cognition, and is therefore a valuable supporting component of the embodied brain theory. Conversely, embodiment might also support the UCT theory and its generalization to other brain regions, as argued in the following section.

3. Embodied cognition supports the UCT theory and its generalization to other brain regions

The previous section posed the UCT theory as a critical element of the embodied brain. Here we explore whether embodied cognition supports the UCT theory. Embodied cognition contextualizes a cerebellum-focused theory within a general neurological theory, that is, the UCT does not represent an isolated example of dependence between motor and non-motor processes in the brain. The hypothesis that a common neurological process underlies cerebellar modulation of movement, thought and emotion is entirely logical in the general context of a brain where sensorimotor, cognitive and affective systems are interdependent.

Additionally, the embodied conception of brain function in which cognitive, affective and sensorimotor systems are not independent supports the possibility that the UCT theory might be generalizable to other brain regions. This possibility emerged from the observation that the cytoarchitecture of the striatum is, like the cerebellum, essentially uniform throughout, and there may be, as in the cerebellum, a common computation performed by the basal ganglia (Alexander & Crutcher, 1990; Schmahmann & Pandya, 2008; Yin, 2014).

A generalization of the UCT to other brain regions would be conceptualized under Schmahmann and Pandya's proposed principles of organization of distributed neural circuits (Schmahmann & Pandya, 2006, 2008). These authors suggested that (i) *architecture determines the transform*, i.e., each anatomically homogenous area within the nervous system performs a distinct universal transform, (ii) *connections define behavior*, i.e., each universal transform is able to operate in different environments, and therefore emerge as different functions, as a result of connections with different areas of the brain, and (iii) association fiber tracts that link cerebral cortical areas with each other enable the cross-modal integration required for evolved complex behaviors.

In this formulation, functional topography in structures with essentially uniform architecture such as the cerebellum and the striatum would be determined by topographical variations in connectivity, rather than in anatomy or physiology. By corollary, functional topography in structures with heterogeneous architecture such as the cerebral cortex or the different nuclei of the thalamus would be analyzed in two steps, namely, architecture and connections. First, anatomical analysis would identify multiple distinct areas within the heterogeneous structure, each performing a distinct universal transform (e.g., each histologically distinct nucleus within thalamus, or each histologically distinct region within the cerebral cortex). Second, a connectivity analysis of each anatomically homogenous area would explore how each universal transform operates in different environments and therefore emerges as different functions, defining the functional topography of each anatomically homogenous area

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(e.g., the functional topography of the cerebellum, of striatum, the pulvinar medialis nucleus of thalamus, or a focal Brodmann area).

The notion that singular anatomically-determined universal transforms can manifest, through connectivity, as sensorimotor, cognitive, and affective functions resonates with the embodiment thesis that cognitive, affective, and sensorimotor systems are not independent. In this way, the UCT theory and its generalization to other brain regions (Schmahmann & Pandya, 2008) becomes contextualized and supported in one of the most important research programs in contemporary cognitive science (Dove, 2016) – embodied cognition.

When viewed from an evolutionary perspective, the hypothesis of the UCT and its generalization to other brain regions resonates with the "neural reuse" hypothesis (Anderson, 2010), which holds that brain regions originally engaged in phylogenetically older functions may have become secondarily engaged in newer functions through the evolution of new connections. Given that older and newer functions might represent sensorimotor and cognitive functions, respectively, it is evident that the neural reuse hypothesis establishes a link between embodied cognition and cognitive evolution. Barton, 2012 directed special attention to embodied cognitive evolution and the cerebellum, noting that "*computational commonality across functional domains with overlapping neural substrates may in fact be a rather generic feature of the brain*", and suggesting that this is because the neural reuse hypothesis may apply not only to the cerebellum but also to other brain regions. In this way, there is an analogy between Barton's argument that an embodied perspective of *brain evolution* explains computational commonalities in brain regions other than the cerebellum, and our argument that an embodied perspective of *brain function* supports the generalization of the UCT hypothesis to brain regions other than the cerebellum.

4. Embodied cognition might shape future definitions of the UCT

Our thesis thus far is that the UCT strengthens the notion of embodied cognition, and that embodied cognition supports the UCT theory and its generalization to other brain regions. Here we present the hypothesis that embodied cognition might shape future definitions of the UCT. To define what is being modulated might have implications for the definition of how this modulation operates – embodiment provides information relevant to the definition of the computation underlying the UCT because it describes the relationship between the neurological systems modulated by the UCT. Restated: The UCT modulates the distributed neural circuits subserving sensorimotor, cognitive, and affective systems; embodied cognition describes the relationship between these three domains. The central tennet of the UCT is that movement, cognition, and affect are *modulated by the cerebellum around a homeostatic baseline, without conscious awareness, and according to context* (Schmahmann, 1996). One interpretation of the relationship between the cerebellum and these major domains of neurological function is that the cerebellum modulates these behaviors without regard to possible interdependence between the domains themselves. It may be useful for future investigations into the nature of the computation underlying the UCT to consider the embodied framework that recognizes a relationship between cognition, affect and sensorimotor systems. Fig. 2 illustrates this approach: A depiction of the computation underlying the UCT (A) without considering embodied cognitive and affective systems may be different from a description of the computation underlying the UCT that respects either a (B) causal or (C) constitutive dependence between these systems.

5. Two different approaches to embodied cognition and the cerebellum: nonmotor deficits after cerebellar injury can be conceptualized as disruption of motor or nonmotor cerebellar functions

The present special issue is focused on the fact that "*damage to motor networks leads to early and even preclinical deficits in two specific language domains: verbs denoting bodily movements and syntax (hierarchical sequencing of words)*", and argues that such a pattern of deficits might help "*understand high-order impairments in motor diseases and even contribute to the latter's preclinical detection*". García, Abrevaya et al., 2017 is a clear example of an application of this logic to the study of cognitive deficits after cerebellar

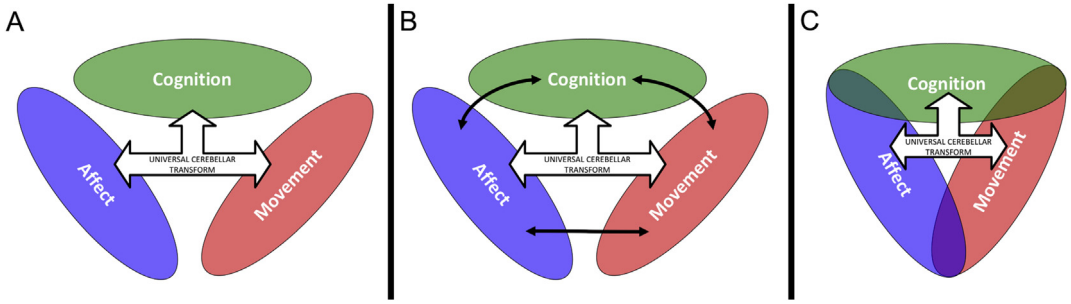

Fig. 2 – Schematic of the argument that an embodied concept of sensorimotor, cognitive, and affective functions might shape future definitions of the Universal Cerebellar Transform. Depiction of the computation underlying the UCT (A) without considering embodied cognitive and affective systems may be different from a description of the computation underlying the UCT that respects either a (B) causal or (C) constitutive dependence between these systems.

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injury: a patient with cerebellar atrophy showed a selective impairment in action verb processing, and the authors argued that this agreed with the conception that damage to motor networks results in specific deficits in the domains of syntax and action semantics (see also Buccino et al., 2017; Cotelli et al., 2007 in the present special issue for an application of this logic when studying behavioral responses in patients with Parkinson's disease; Marino et al., 2014 for an example of the same logic when analyzing behavioral responses in healthy subjects; Bak & Hodges, 2004 for motor neurone disease; and York et al., 2014 for amyotrophic lateral sclerosis).

In the present article we have adopted a different, complementary approach. A sizable body of multidisciplinary evidence indicates that some parts of the cerebellum are engaged in motor processing while others are selectively dedicated to cognitive and affective functions (Stoodley & Schmahmann, 2009; Schmahmann, Macmore, & Vangel, 2009; Stoodley et al., 2012; E et al., 2014; Stoodley et al., 2016). We have conceptualized cognitive deficits after cerebellar injury as the manifestation of damage to the cerebellar regions which are preferentially involved in cognitive processing. This is not to say, however, that cognitive deficits resulting from cerebellar injury cannot be understood, from our perspective, as "*embodiment disrupted*" (as the title of the present special issue reads). This is because, as we have argued, there is a UCT underlying cerebellar modulation of movement, thought and emotion; and a universal cerebellar impairment (dysmetria) that dictates the logic of motor, cognitive and affective deficits after cerebellar injury.

In this way, the embodied cognition research program can approach the cerebellum from two different, not mutually exclusive perspectives. One, as exemplified in García, Abrevaya et al., 2017, is to visualize cognitive deficits after cerebellar injury as the disruption of a *motor* cerebellar function, and to consider this in conjunction with the thesis that some aspects of cognitive processing (syntax and action semantics) are interdependent with the motor cerebellum. This approach results, accordingly, in a study focused on syntax and action semantics impairments after cerebellar injury. A different approach, as developed in the present article, is to visualize cognitive deficits after cerebellar injury as a disruption a *cognitive* cerebellar function, and to consider this in conjunction with the UCT and Dysmetria of Thought theories. This perspective leads to a study of cognitive and affective impairments that follow the logic of motor problems after cerebellar injury (e.g. metalinguistic deficits [Guell et al., 2015] and hypo/hypermetric neuropsychiatric manifestations [Schmahmann et al., 2007]).

Both approaches are potentially relevant for the diagnosis and management of cognitive and affective deficits after cerebellar injury. On the one hand, it has been argued that grammar and semantics expressing motor content may help in the early diagnosis and management of motor diseases (e.g., Buccino et al., 2017; García, Sedeño et al., 2017). Given that the cerebellum is likely part of the motor system that is interleaved with action semantics and syntax processing, this reasoning applies to the cerebellum. On the other hand, the UCT and Dysmetria of Thought hypotheses also inform the diagnosis and management of cerebellar injury. They guide the formation of hypotheses regarding the nature of cognitive and affective impairments that follow cerebellar damage: thus for example, regulation of the speed, capacity, consistence and appropriateness of emotions, following the logic of alterations in the rate, rhythm and accuracy of movement. They also implicate cerebellum in the pathophysiology of the core neurobehavioral phenomena of what is now recognized as the CCAS, such as deficits in executive control, language (grammar, syntax, metalinguistics, and action semantics), visual spatial processing, and emotion regulation. This has implications for a potential neurological basis to the diagnosis (i.e., cerebellar posterior lobe injury) in patients who present with an essentially normal motor examination but with cognitive and/or neuropsychiatric manifestations previously believed to indicate damage to the cerebral association cortices. Further, the concept of Dysmetria of Thought informs patients and their families regarding the non-motor problems that a person with ataxia may experience. This includes challenges with cognitive multitasking and the need to bring mental processes to conscious awareness, following the logic of impaired motor multitasking and the need to be consciously aware of motor actions. The ideas of a UCT and Dysmetria of Thought may also guide the development of cognitive training programs and other therapeutic interventions for the CCAS, an emerging area of focus in the management of patients with cerebellar damage.

6. Conclusion

We have analyzed the relationship between embodied cognition, the UCT, and Dysmetria of Thought and stated that (i) the UCT strengthens the notion of embodied cognition, (ii) embodied cognition supports the UCT theory, (iii) embodied cognition supports the generalization of the UCT to other brain regions, and (iv) embodied cognition might shape future definitions of the UCT. These arguments highlight the relevance of the UCT theory for the embodied cognition research program, the need to consider embodiment theses in cognitive cerebellar research, and the importance of conducting experiments aimed at directly testing the UCT hypothesis.

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