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**Universitat Autònoma  
de Barcelona**

**PhD THESIS**

**THE ROLE OF THE CEREBELLUM IN MOVEMENT, THOUGHT, AND  
EMOTION**

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Barcelona, 2018

## **INDEX**

1. Abstract, Catalan translation of the abstract, Spanish translation of the abstract
2. Introduction and objectives
3. Studies
  - 3.1. Study I. Metalinguistic Deficits In Patients With Cerebellar Dysfunction: Empirical Support For The Dysmetria Of Thought Theory.
  - 3.2. Study II. The cerebellar cognitive affective syndrome / Schmahmann syndrome scale.
  - 3.3. Study III. Embodied cognition and the cerebellum: Perspectives from the Dysmetria of Thought and the Universal Cerebellar Transform theories.
  - 3.4. Study IV. Triple representation of language, working memory, social, and emotion processing in the cerebellum: convergent evidence from task and seed-based resting-state fMRI analyses in a single large cohort.
  - 3.5. Study V. Functional gradients of the cerebellum: a fundamental movement-to-thought principle.
4. General discussion, conclusions, and future directions
5. References corresponding to sections 2 and 4

## 1. ABSTRACT

Evidence from multiple fields of study has established that the cerebellum is involved in motor, cognitive, and affective processes. Anatomical studies reveal cerebellar connections to motor and non-motor extracerebellar territories; cerebellar injury or degeneration results in a cerebellar motor syndrome but also in a cerebellar cognitive/affective syndrome; neuroimaging studies reveal cerebellar activation in motor and nonmotor processes; and many studies have reported cerebellar abnormalities in numerous neurological and psychiatric diseases that degrade cognition and affect.

The compendium of studies that are included in this thesis present the following advances in our understanding of the role of the cerebellum in movement, thought, and emotion: (i) evidence supporting the presence of executive, linguistic, visual spatial, and affective impairments that characterize the Cerebellar Cognitive Affective syndrome, (ii) the description of similarities between linguistic and motor deficits in cerebellar dysfunction, which reinforces the notion of that a uniform computation underlies the cerebellar modulation of movement, thought, and emotion (Universal Cerebellar Transform theory), (iii) a review of the supporting evidence and relevance of the Universal Cerebellar Transform theory, (iv) confirmatory evidence of the presence and arrangement of functionally specialized motor and nonmotor regions of the cerebellum, which reaffirms the anatomical principles that underlie the notion of a Universal Cerebellar Transform, (v) the novel description of triple representation of non-motor task processing in the cerebellum, unmasking new clinical and basic science questions, and (vi) the discovery of a fundamental movement-to-thought principle of cerebellar macro-scale organization, which can serve as a guiding framework for future cerebellar research across neuroscience disciplines.

## CATALAN TRANSLATION OF THE ABSTRACT

Evidència derivada de múltiples camps d'estudi ha establert que el cerebel està involucrat en funcions motores, cognitives, i afectives. Estudis anatòmics revelen que el cerebel està connectat a zones motores i no motores dels territoris extra-cerebel·losos; lesió o degeneració del cerebel genera una síndrome motora cerebel·losa però també una síndrome cognitiva i afectiva cerebel·losa; estudis de neuroimatge revelen activació del cerebel en processos motors i no motors; i molts estudis han descrit anormalitats cerebel·loses en nombroses malalties neurològiques i psiquiàtriques que alteren la cognició i les emocions.

El compendi d'estudis que s'inclou en aquesta tesi presenta els següents avanços en la comprensió del rol del cerebel en processos motors, cognitius, i afectius: (i) evidència que recolza la presència d'anormalitats en funcions executives, lingüístiques, visuals-espacials, i afectives que caracteritzen la síndrome cognitiva i afectiva cerebel·losa, (ii) la descripció de similituds entre dèficits motors i lingüístics en pacients amb malalties cerebel·loses, que reforça la idea que hi ha una computació uniforme que subjau la modulació cerebel·losa dels processos motors, cognitius, i afectius ("Universal Cerebellar Transform theory"), (iii) una revisió de la rellevància i l'evidència que suporta la "Universal Cerebellar Transform theory", (iv) evidència confirmatòria per la presència i distribució de regions funcionals cerebel·loses motores i no motores, que reafirma els principis anatòmics que subjauen la "Universal Cerebellar Transform theory", (v) la descripció d'una triple representació de tasques no motores en el cerebel, revelant noves preguntes clíniques i científiques, (vi) el descobriment d'un principi fonamental de "movement-to-thought" en la macro-organització del cerebel, que pot servir com a marc guia per futures investigacions sobre el cerebel en diferents disciplines neurocientífiques.

## SPANISH TRANSLATION OF THE ABSTRACT

Evidencia derivada de múltiples campos de estudio ha establecido que el cerebelo está involucrado en funciones motoras, cognitivas, y afectivas. Estudios anatómicos revelan que el cerebelo está conectado a zonas motoras y no motoras de territorios extra-cerebelosos; lesión o degeneración del cerebelo genera un síndrome motor cerebeloso pero también un síndrome cognitivo y afectivo cerebeloso; estudios de neuroimagen revelan activación del cerebelo en procesos motores y no motores; y muchos estudios han descrito anomalías cerebelosas en numerosas enfermedades neurológicas y psiquiátricas que alteran la cognición y las emociones.

El compendio de estudios que se incluye en esta tesis presenta los siguientes avances en nuestra comprensión del rol del cerebelo en procesos motores, cognitivos, y afectivos: (i) evidencia que apoya la presencia de anomalías en funciones ejecutivas, lingüísticas, visual-espaciales, y afectivas que caracterizan el síndrome cognitivo y afectivo cerebeloso, (ii) la descripción de similitudes entre anomalías motoras y lingüísticas en pacientes con enfermedades cerebelosas, que refuerza la idea de que hay una computación uniforme que subyace la modulación cerebelosa de los procesos motores, cognitivos, y afectivos (“Universal Cerebellar Transform theory”), (iii) una revisión de la relevancia y la evidencia que soporta la “Universal Cerebellar Transform theory”, (iv) evidencia confirmatoria de la presencia y la distribución de regiones funcionales cerebelosas motoras y no motoras, que reafirma los principios anatómicos que subyacen la “Universal Cerebellar Transform theory”, (v) la descripción de una triple representación de procesos no motores en el cerebelo, revelando nuevas preguntas clínicas y científicas, (vi) el descubrimiento de un principio fundamental de “movement-to-thought” en la macro-organización del cerebelo, que puede servir como marco guía para futuras investigaciones sobre el cerebelo en distintas disciplinas neurocientíficas.

## 2. INTRODUCTION AND OBJECTIVES

Observations from anatomical, clinical, behavioral, and neuroimaging studies indicate that the human cerebellum is engaged not only in motor control but also in cognitive and affective processing. Tract tracing investigations revealed anatomical connections between the cerebellum and motor as well as non-motor extracerebellar structures, clinical observations and neuropsychological testing showed motor as well as cognitive/affective abnormalities in patients with cerebellar injury or degeneration, and numerous neuroimaging investigations have described cerebellar engagement in motor as well as nonmotor aspects of task processing and functional connectivity.<sup>1-20</sup> In addition, structural and functional cerebellar abnormalities have been identified in many psychiatric and neurological diseases that impair cognition and affect - these include major depressive disorder, anxiety disorders, bipolar disorder, schizophrenia, attention deficit and hyperactivity disorder, autism spectrum disorders, posttraumatic stress disorder, fibromyalgia, Alzheimer's disease, frontotemporal dementia, vascular dementia, Huntington's disease, multiple sclerosis, and Parkinson's disease.<sup>21-28</sup> The cerebellum has thus become scientifically relevant not only for the study of motor processing, but for also for the investigation of all complex neurological functions. Similarly, the cerebellum is now clinically relevant not only for the study of primary cerebellar injury or degeneration, but also for Neurology and Psychiatry as a whole.

In this way, the present thesis is situated in a context where the cerebellum is receiving increased attention as a necessary component for understanding the nervous system and alleviating suffering in neurological and psychiatric conditions. The previous decades have witnessed a paradigm shift in the appreciation of the basic and clinical neuroscience of the cerebellum<sup>29</sup>. At the same time, the cerebellum remains an understudied area of the brain<sup>30</sup>, and many questions remain to be answered<sup>31</sup>.

The compendium of studies presented here reflects on two fundamental pillars of cerebellar neuroscience - behavior and neuroimaging. Clinical aspects of cerebellar cognitive neuroscience are also discussed, but in the present work remain linked and subordinated to a more general discussion of basic cerebellar neuroscience. The present thesis revolves around two objectives: (i) to characterize and discuss the nature of behavioral abnormalities in

cerebellar dysfunction, and (ii) to describe the functional organization of the cerebellum. These two objectives are not independent, but rather deeply intertwined. Behavioral deficits shed light into the nature of cerebellar motor and nonmotor processing. At the same time, the presence and arrangement of motor and nonmotor cerebellar functional subregions is fundamentally connected to the anatomical realities that inspire our cerebellar cognitive theories.

Specifically, the studies that follow aim to address the following questions:

i) How can we characterize linguistic abnormalities in cerebellar dysfunction? What does this teach us regarding the nature of the cerebellar contribution to motor, cognitive, and affective processing?

ii) Building on the initial description of the Cerebellar Cognitive Affective Syndrome, can we replicate and expand the characterization of nonmotor deficits in cerebellar patients? Based on this knowledge, can we develop a clinical tool to identify this syndrome in a fast, sensitive, and specific manner?

iii) After carefully examining behavior in cases of cerebellar dysfunction, we analyzed the cognitive theories that describe the cerebellar role in movement, thought, and emotion. How can we conceptualize the cerebellar participation in these domains?

iv) The presence and arrangement of motor and nonmotor cerebellar functional subregions is crucial to our understanding of the role of the cerebellum in movement, thought, and emotion. Can we replicate and expand previous descriptions of cerebellar functional topography?

v) While we succeeded at replicating and expanding previous descriptions of cerebellar functional topography, we realized that all studies of cerebellar functional organization have divided the cerebellum into discrete parcels. Can we describe what the relationship between cerebellar regions that fall across distinct networks is, and do this following a gradient-based approach?



vi) We described a triple representation of non-motor task processing in the cerebellum, analogous to the well-established concept of double motor representation. However, we could not describe any functional characteristics of this organization. What is the relationship between the two motor and three nonmotor areas of representation, and what are the differences between each area of representation?

The studies presented in section 3 will address these questions. Each study header will specify which question is addressed. Section 4 will recapitulate these questions, and analyze how the compendium of works presented in this thesis advances our understanding of the cerebellar role in movement, thought, and emotion.

### **3. STUDIES**

#### **3.1. STUDY I. METALINGUISTIC DEFICITS IN PATIENTS WITH CEREBELLAR DYSFUNCTION**

*Guell, X., Hoche F., Schmahmann, J.D. (2015). Metalinguistic Deficits in Patients with Cerebellar Dysfunction: Empirical Support for the Dysmetria of Thought Theory. Cerebellum, 14, 50-58.*

DOI: 10.1007/s12311-014-0630-z

#### **Question addressed:**

**i) How can we characterize linguistic abnormalities in cerebellar dysfunction? What does this teach us regarding the nature of the cerebellar contribution to motor, cognitive, and affective processing?**

### **3.2. STUDY II. THE CEREBELLAR COGNITIVE AFFECTIVE SYNDROME / SCHMAHMANN SYNDROME SCALE**

*Hoche, F., Guell, X., Vangel, M.G., Sherman, J.C., Schmahmann, J.D. (2018). The cerebellar cognitive affective/Schmahmann syndrome scale. Brain, 141(1), 248-270.*

*DOI: 10.1093/brain/awx317*

#### **Question addressed:**

**ii) Building on the initial description of the Cerebellar Cognitive Affective Syndrome, can we replicate and expand the characterization of nonmotor deficits in cerebellar patients? Based on this knowledge, can we develop a clinical tool to identify this syndrome in a fast, sensitive, and specific manner?**

### **3.3. STUDY III. EMBODIED COGNITION AND THE CEREBELLUM: PERSPECTIVES FROM THE DYSMETRIA OF THOUGHT AND THE UNIVERSAL CEREBELLAR TRANSFORM THEORIES**

*Guell, X., Gabrieli, J.D.E., Schmahmann, J.D. (2017). Embodied cognition and the cerebellum: Perspectives from the Dysmetria of Thought and the Universal Cerebellar Transform theories. Cortex (in press).*

*DOI: 10.1016/j.cortex.2017.07.005*

**Question addressed:**

**iii) After carefully examining behavior in cases of cerebellar dysfunction, we analyzed the cognitive theories that describe the cerebellar role in movement, thought, and emotion. How can we conceptualize the cerebellar participation in these domains?**

### **3.4. STUDY IV. TRIPLE REPRESENTATION OF LANGUAGE, WORKING MEMORY, SOCIAL, AND EMOTION PROCESSING IN THE CEREBELLUM.**

*Guell, X., Gabrieli, J.D.E., Schmahmann, J.D. (2018). Triple representation of language, working memory, social and emotion processing in the cerebellum: convergent evidence from task and seed-based resting-state fMRI analyses in a single large cohort. Neuroimage (in press).*

DOI: [10.1016/j.neuroimage.2018.01.082](https://doi.org/10.1016/j.neuroimage.2018.01.082)

**Question addressed:**

**iv) The presence and arrangement of motor and nonmotor cerebellar functional subregions is crucial to our understanding of the role of the cerebellum in movement, thought, and emotion. Can we replicate and expand previous descriptions of cerebellar functional topography?**

### **3.5. STUDY V. FUNCTIONAL GRADIENTS OF THE CEREBELLUM: A FUNDAMENTAL MOVEMENT-TO-THOUGHT PRINCIPLE.**

*Guell, X., Schmammann, J.D., Gabrieli, J.D.E., Ghosh, S.S. (2018). Functional gradients of the cerebellum: a fundamental movement-to-thought principle. Biorxiv.*

DOI: 10.1101/254326.

#### **Question addressed:**

**v) While we succeeded at replicating and expanding previous descriptions of cerebellar functional topography, we realized that all studies of cerebellar functional organization have divided the cerebellum into discrete parcels. Can we describe what the relationship between cerebellar regions that fall across distinct networks is, and do this following a gradient-based approach?**

**vi) We described a triple representation of non-motor task processing in the cerebellum, analogous to the well-established concept of double motor representation. However, we could not describe any functional characteristics of this organization. What is the relationship between the two motor and three nonmotor areas of representation, and what are the differences between each area of representation?**

#### **4. DISCUSSION, CONCLUSIONS, AND FUTURE DIRECTIONS**

In this section we will recapitulate the questions outlined in section 2, and analyze how the studies presented in section 3 contributed to their resolution.

**i) How can we characterize linguistic abnormalities in cerebellar dysfunction? What does this teach us regarding the nature of the cerebellar contribution to motor, cognitive, and affective processing?**

In Study I we have shown that linguistic deficits follow the logic of motor deficits in cerebellar dysfunction. In this way, our study supports the concept that a uniform mechanism (the Universal Cerebellar Transform) underlies the cerebellar modulation of movement, thought, and emotion.

**ii) Building on the initial description of the Cerebellar Cognitive Affective Syndrome, can we replicate and expand the characterization of nonmotor deficits in cerebellar patients? Based on this knowledge, can we develop a clinical tool to identify this syndrome in a fast, sensitive, and specific manner?**

In Study II we have provided confirmatory evidence of the characteristics of the Cerebellar Cognitive Affective Syndrome in the largest cohort of patients studied to date, and developed the Cerebellar Cognitive Affective / Schmahmann Syndrome Scale. In addition to its usefulness in the clinical setting, this brief scale offers an unprecedented tool for research studies involving patients with cerebellar injury or degeneration.

**iii) After carefully examining behavior in cases of cerebellar dysfunction, we analyzed the cognitive theories that describe the cerebellar role in movement, thought, and emotion. How can we conceptualize the cerebellar participation in these domains?**

In Study III we have provided an extensive and updated discussion on the supporting anatomical, behavioral, and neuroimaging evidence and relevance of the Dysmetria of

Thought and the Universal Cerebellar Transform theories, in addition to an analysis of their relationship with the embodied cognition research program.

**iv) The presence and arrangement of motor and nonmotor cerebellar functional subregions is crucial to our understanding of the role of the cerebellum in movement, thought, and emotion. Can we replicate and expand previous descriptions of cerebellar functional topography?**

In Study IV we have replicated previous descriptions of cerebellar motor and nonmotor functional topography, and described for the first time a triple representation of non-motor task processing in the cerebellum. The concept of a triple representation of non-motor function in the cerebellum is inspired by the well-established notion of double representation of motor processing.

**v) While we succeeded at replicating and expanding previous descriptions of cerebellar functional topography, we realized that all studies of cerebellar functional organization have divided the cerebellum into discrete parcels. Can we describe what the relationship between cerebellar regions that fall across distinct networks is, and do this following a gradient-based approach?**

In Study V we have described, for the first time, that cerebellar functional regions follow a gradual organization from motor to transmodal (task-unfocused) regions. This simple, powerful description identifies a new and fundamental principle of cerebellar macroscale function which can serve as a guiding framework for future cerebellar research across neuroscience disciplines.

**vi) We described a triple representation of non-motor task processing in the cerebellum, analogous to the well-established concept of double motor representation. However, we could not describe any functional characteristics of this organization. What is the relationship between the two motor and three nonmotor areas of representation, and what are the differences between each area of representation?**



In Study V we have described, by using a gradient basis for function, a functional property of the double motor and triple nonmotor representation organization of the cerebellum. Specifically, we show that the second motor representation shares functional characteristics with the third nonmotor representation. This description introduces novel testable hypotheses to the investigation of the double motor / triple nonmotor organization.

Taken together, the compendium of publications presented here offers behavioral and neuroimaging observations that advance our understanding of the role of the cerebellum in movement, thought, and emotion. The confirmation of the executive, linguistic, visual spatial, and affective impairments that characterize the Cerebellar Cognitive Affective syndrome represents an anchor point for future characterizations, and potential interventions, of cognitive and affective abnormalities in cerebellar patients. Delving into the nature of cerebellar motor and nonmotor processing, the description of a similarity between linguistic and motor deficits in cerebellar dysfunction reinforces the notion of a Universal Cerebellar Transform. Careful analysis of the supporting evidence and relevance of this theory highlights the importance of conducting experiments to directly test the Universal Cerebellar Transform hypothesis. Deeply linked with the concept of the Universal Cerebellar Transform and our understanding of the cerebellar role in movement, thought, and emotion, the confirmation of the presence and arrangement of functionally specialized regions of the cerebellum reaffirms the anatomical duality (uniform cytoarchitecture, and heterogeneity of connectivity) that underlies the Universal Cerebellar Transform hypothesis. In addition, the description of a triple representation of non-motor task processing unmask novel questions which might become critical for the understanding of cerebellar physiology and pathophysiology. These questions include the need to investigate the distinct consequences of injury to each area of nonmotor representation, the analysis of a potential preferential mapping of structural or functional abnormalities in psychiatric diseases to one of these areas of representation, or the examination using task contrast analyses of preferential engagement of a particular nonmotor representation in a particular task characteristic. Our gradients analysis provides an initial observation regarding the functional significance of the double motor / triple nonmotor organization - specifically, we hypothesize that third nonmotor representation might share functional characteristics with the second motor representation. Future studies might directly test this possibility. At a more general level, our gradients analysis unmask a fundamental

movement-to-thought organization property of the cerebellum, describing for the first time the relationship between cerebellar regions that fall across distinct networks. The primary-to-transmodal concept<sup>32</sup> has greatly influenced topographical investigations in the cerebral cortex, and it is reasonable to consider that the present gradient description in the cerebellum may equally influence future cerebellar investigations.

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