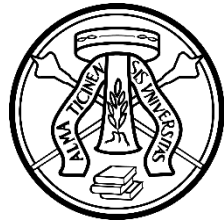


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Department of Brain and Behavioral Sciences (DBBS)  
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## Contributions of posterior lateral cerebellum to facial emotion recognition: Chronometric TMS study

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# Abstract

The cerebellum, traditionally known for its role in motor processing, has recently emerged as a critical structure in social and affective processing, with distinct subsections contributing to various functions. In this study, we employed chronometric transcranial magnetic stimulation (TMS) to investigate the temporal dynamics of the posterior lateral cerebellum's involvement in affective processing. Twenty participants engaged in a two-alternative forced choice task, where they were sequentially presented with pairs of faces depicting primary emotions. They were asked to determine whether the two faces expressed the same emotion, while a triple-pulse 20 Hz chronometric TMS was applied to the posterior lateral cerebellum. Our findings indicate that the posterior lateral cerebellum is involved in the early stages of emotional processing, approximately 100 milliseconds after stimulus onset, within the same time window as the medial posterior cerebellum, as identified in our previous study. These results provide causal evidence for the parallel processing of affective stimuli by distinct regions of the posterior cerebellum.

Keywords: cerebellum, emotions, chronometry, transcranial magnetic stimulation (TMS), parallel processing.



# Introduction

The cerebellum, in literal translation, means “little brain”. In comparison to our large primate brain, it might indeed appear small. However, it contains approximately 60% of all neurons in the brain (Herculano-Houzel, 2010). Furthermore, it houses one of the biggest neurons in the brain, the Purkinje cell. The intricate arborization of Purkinje cells, as depicted by Ramón y Cajal—one of the pioneers of modern neuroscience—remains prominently displayed in many textbooks as a subject of fascination. Historically, the cerebellum was primarily regarded as crucial for motor functions. In the 19th century, it was first proposed that the cerebellum plays a role in motor control based on observations that patients experienced immediate difficulties in movement coordination following cerebellar resection. This hypothesis was further substantiated during World War I when English neurologist Gordon Holmes, reporting directly from the frontlines, noted that soldiers with cerebellar injuries exhibited significant motor coordination problems (Bower & Parsons, 2003).

Indeed, the classical view of the cerebellar function was confined to automating and smoothing movements. Jeremy Schmahmann's groundbreaking work, however, convinced the field that the cerebellum plays a role not only in refining our movements but also in shaping our thoughts. Nowadays, it is firmly established that the cerebellum is not only involved in our everyday lives by correcting movements, but also our language, thinking or ability to navigate our complex social lives. Emerging evidence points towards the importance of the cerebellum in many disorders, such as depression or autism spectrum disorders, suggesting that the cerebellum might have been the missing link in our understanding of these debilitating conditions.

Sociality is one of the key factors that distinguish humans from other animals. In this thesis, we will explore the cerebellum's role in social cognition, particularly in understanding the minds and emotions of others. We will begin by outlining the physiology and anatomy of the cerebellum in the first chapter to establish the neural machinery underlying its functions. The second chapter will address the traditional view of the cerebellum's involvement in motor functions. In the third chapter, we will shift our focus to the non-motor functions of the cerebellum, discussing major theories related to its broader role. Following this, we will explore social cognition, and the major cerebral networks involved, highlighting how the cerebellum contributes to these processes.



Finally, in the last chapter, we will introduce the central topic of our thesis: the cerebellum's contributions to affective processing.

# 1 Anatomy and physiology of the cerebellum

The cerebellum is a highly convoluted posterior subcortical structure comprised of the cerebellar cortex, which is divided into two hemispheres. The cerebellar cortex consists of grey matter, internal white matter, and three pairs of subcortical nuclei: the fastigial nucleus, the interposed nucleus (comprising of emboliform and globose nuclei), and the dentate nucleus.

The cerebellum is connected to the rest of the brain by three pairs of peduncles (D'Angelo, 2018):

- A) inferior cerebellar peduncle (restiform body),
- B) middle cerebellar peduncle (brachium pontis),
- C) superior cerebellar peduncle (brachium conjunctivum).

The cerebellum receives inputs from (D'Angelo, 2018):

- 1) cerebral cortex,
- 2) brain stem nuclei, superior and inferior colliculi, vestibular nuclei, reticular formation and inferior olive,
- 3) spinal cord nuclei.

In Schmahmann's MRI Atlas of the Human Cerebellum (2000), the cerebellum is meticulously subdivided into four major divisions, each with distinct anatomical and functional characteristics (Figure 1). These subdivisions provide a comprehensive framework for understanding the cerebellum's complex structure and its role in coordinating motor and cognitive functions.

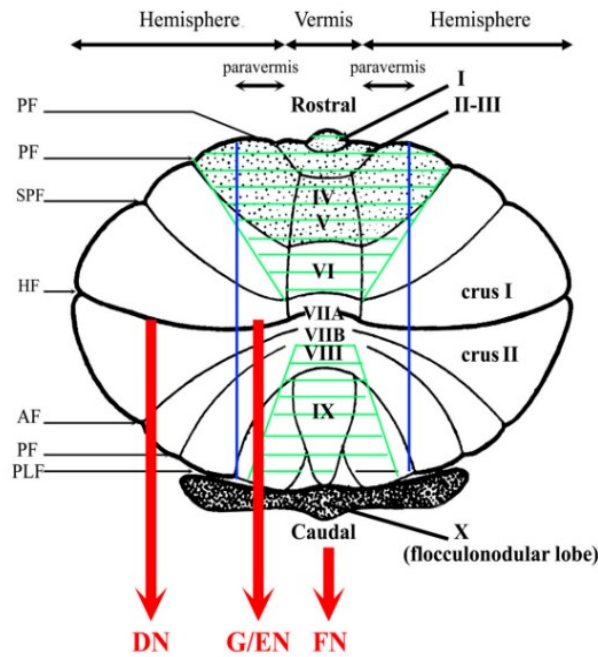


Figure 1. Diagram of flattened cerebellar surface. Four major subdivisions (Schmahmann et al., 2000): (1) Division in lobes: anterior lobe (gray stippling), posterior lobe, and flocculonodular lobe; (2) (Para-)sagittal division: vermis, and left and right hemispheres, which are further divided into the paravermis and the lateral parts of the hemispheres; and (3) Phylogenetic division: archicerebellum (flocculonodular lobe in dark), paleocerebellum (green hatching), and neocerebellum (in white). The cerebellar cortex in the vermal, paravermal, and lateral hemispheric divisions projects to the fastigial (FN), globose/emboliform (G/EN), and dentate nuclei (DN), respectively. AF, Ansa paramedian fissure; HF, horizontal fissure; PLF, posterolateral fissure; PF, precentral fissure; PpF, prepyramidal fissure; PrF, primary fissure; SPF, and superior posterior fissure (Habas et al., 2009).

## 1. Lobar Division

The cerebellum is divided into lobes: the anterior lobe, the posterior lobe, the flocculonodular lobe and lobules numbered from I to X. The anterior cerebellum, coined as the sensorimotor cerebellum, comprised of lobules I-V, is mainly involved in the motor related tasks, whereas the posterior cerebellum, comprised of lobules VI-IX, is involved primarily in affective and higher cognitive functions (Kelly & Strick, 2003; Middleton & Strick, 2001; Schmahmann, 2001; Stoodley & Schmahmann, 2009). Lastly, the flocculonodular lobe, a small yet significant structure, plays a key role in balance and eye movements (D'Angelo, 2018).

## 2. (Para-)Sagittal Division

This division segments the cerebellum along a sagittal plane, categorizing it into the vermis and the left and right hemispheres. The vermis, located at the midline, is primarily associated with the coordination of axial muscles. The hemispheres are further subdivided into the paravermis, which lies adjacent to the vermis, and the lateral parts of the

hemispheres. Novel evidence suggests that the posterior vermis is primarily involved in low-level affective and cognitive functions, whereas the posterior lateral cerebellum is subserving high-level cognitive processing (Ferrari et al., 2023).

### **3. Phylogenetic Division**

Furthermore, the cerebellum can be classified based on its evolutionary development, into the archicerebellum, paleocerebellum, and neocerebellum. The archicerebellum, comprised of the flocculonodular lobe, is the most primitive part of the cerebellum, appearing first in fish together with anterior vermis. It contributes to the maintenance of balance, vestibulo-ocular reflexes and eye movements. It receives efferents from the vestibular and visual areas. Impairments of the archicerebellum result in disrupted body balance and control of the eye movements (D'Angelo, 2018).

The paleocerebellum consists of the vermis and the medial regions of the hemispheres. The vermis processes somatosensory inputs from the head and proximal regions of the body, in addition to visual, auditory, and vestibular inputs. The vermis plays a crucial role in locomotion, postural maintenance, and eye movements. The intermediate regions of the hemispheres, located adjacent to the vermis, receive somatosensory inputs from the limbs and project to the corticospinal and rubrospinal systems, thus contributing to the control of limb movements (D'Angelo, 2018). Together with its functions in motor control, converging evidence points to the importance of the vermis in affective processing (Adamaszek et al., 2017).

The neocerebellum is the phylogenetically youngest part of the cerebellum comprised of lateral parts of the cerebellar hemispheres. The lateral hemispheres seem to extensively participate in planning and executing movements as well as cognitive functions (Habas, 2021; Stoodley & Schmahmann, 2009).

### **4. Projection Pathways**

Schmahmann's atlas also details the projection pathways from the cerebellar cortex to the deep cerebellar nuclei. The deep cerebellar nuclei (DCN) constitute a main output from the cerebellum which contacts the cerebrum and brain stem through the superior cerebellar peduncle. DCN establishes connections to various brain stem nuclei (reticular formation, red nucleus, vestibular nucleus and inferior olive) or to the cortex via the thalamus (D'Angelo, 2018). The archicerebellum, projects to the vestibular nucleus in the brain stem.

The vermis projects to the fastigial nucleus (FN) which subsequently relays its inputs to cortical and brainstem regions, thereby establishing medial descending pathways that govern the proximal muscles of the body and limbs.

The paravermal region projects to the globose and emboliform nuclei (G/EN), and the lateral hemispheres to the dentate nucleus (DN) contacting primarily motor, premotor and prefrontal cortices (Kelly & Strick, 2003; Middleton & Strick, 2001). These pathways are crucial for understanding how the cerebellum integrates sensory and motor information to produce smooth, coordinated movements.

In addition to these subdivisions, the atlas identifies several key longitudinal fissures that delineate the cerebellar structure (Figure 1). Anterior and posterior lobes of the cerebellum form its main body and are separated by the primary fissure (PrF) located on its dorsal surface. Flocculonodular lobe, the most primitive is separated from the rest of the cerebellum by the posterolateral fissure (PLF) located on the ventral surface (Cerminara et al., 2015). Additionally, the ansoparamedian fissure (AF), horizontal fissure (HF), precentral fissure (PF), prepyramidal fissure (PpF) and superior posterior fissure (SPF), separate individual cerebellar lobules.

This detailed anatomical breakdown according to Schmähmann et al. (2000) provides a foundational understanding of the cerebellum's structure, essential for studying its role in both motor control and higher cognitive functions.

## 1.1 Cerebellar cytoarchitecture

Neurons in the cerebellar cortex are organized within three layers, each containing a distinct type of neuron and performing different functions. Figure 2 depicts a diagram of cerebellar cytoarchitecture, with different types of cells, connections, and input fibres.

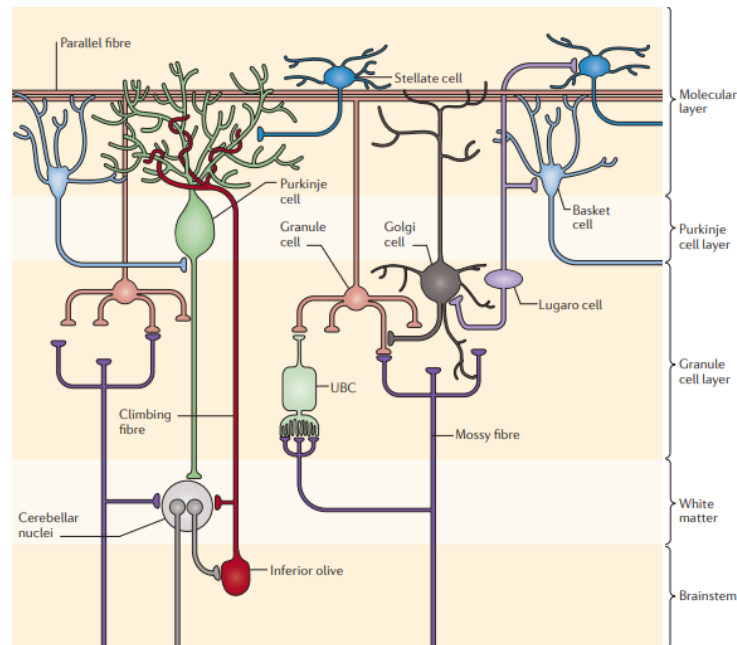


Figure 2. Cerebellar cytoarchitecture. UBCs, unipolar brush cells (Cermignani et al., 2015).

### A) Granular layer

The innermost neuronal layer, known as the granular layer, serves as the input layer and is predominantly composed of granule cells, which exhibit an exceptionally high density, constituting approximately half of the brain's neurons (Ekerot & Jörntell, 2008). The axons of granule cells extend to the outermost molecular layer, which also contains a limited number of larger Golgi interneurons characterized by two distinct dendritic trees. One of these trees extends into the molecular layer to contact parallel fibers, while the other descends to form glomeruli, where they provide inhibitory inputs (Marr, 1969). As inhibitory interneurons, Golgi cells are believed to play a crucial role in regulating granule cell activity (D'Angelo et al., 2013). In certain cerebellar regions, additional neuronal types, such as Lugaro, unipolar brush or chandelier cells, can also be found within the granular layer. Mossy fibers, which are among the primary afferent fibers, terminate in this layer, connecting to cerebellar glomeruli composed of granule and Golgi cells, where they deliver excitatory input (Marr, 1969).

## **B) Purkinje cell layer**

This is the middle layer of the cerebellar cortex located between the granule and molecular *layer*, which houses the biggest neuron found in the human brain - the Purkinje neurons (Llinás, 2011). Purkinje neurons are the points of convergence of the whole neuronal activity generated by both molecular and granular layers (Eccles, 1967). Their immaculate arborization traverses into the molecular layer, where they receive inputs from climbing fibres (CF), the second afferent fibre in the cerebellum. Each Purkinje cell is innervated by a single CF and this connection constitutes the most powerful excitatory synapse in the brain (Eccles et al., 1966). As mentioned above, Purkinje neurons are projecting mainly to deep cerebellar nuclei and the vestibular nuclear complex in the brain stem forming inhibitory GABAergic synapses (Teune et al., 1998).

## **C) Molecular layer**

The molecular layer is the outermost layer. It contains cell bodies and dendrites of stellate and basket cells, two important inhibitory neurons as well as dendrites of Purkinje cells and axons of granule cells. Axons of the granule cells are referred to as parallel fibres, since they run parallel to the long axis i.e. medial to lateral direction of the folia. Each Purkinje neuron receives connections from 200 000 to 1 million granule cells (Marr, 1969).

## **1.2 Extracerebellar inputs**

In the cerebellar cortex, Purkinje cells receive two main extracerebellar inputs: the mossy fibres, through granule cells, and CF (Eccles et al. 1967). Both of these fibres are excitatory (Marr, 1969).

A) Mossy fibres represent the main input into cerebellum, terminating in the granular layer (Figure 2), providing sensory and motor related information (De Schutter & Bjaalie, 2001). They originate in various brain stem nuclei (D'Angelo et al., 2016), however the majority of mossy fibre originate in the basilar pontine nuclei (BPN) (Brodal & Bjaalie, 1992). Mossy fibre axons form excitatory synapses on the granule cells in the granular layer, where they are channeling sensory information from the periphery together with information from the cerebral cortex.

Each granule cell receives afferents from three to five mossy fibres (Ekerot & Jörntell, 2008). The granule cells extend their axons into the molecular layer which allows a widespread distribution of information provided by the mossy fibres (Marr, 1969).

B) Climbing fibres convey sensory information from periphery and cerebral cortex, originating in the inferior olivary nucleus (Campbell & Armstrong, 1983; Courville & Faraco-Cantin, 1978) and terminating in the molecular and Purkinje cell layer where they enwrap the cell bodies and proximate axons of the Purkinje cells (Eccles et al., 1967) to which they provide powerful excitatory input (Marr, 1969). These synaptic connections are the largest synaptic junctions in the vertebrate central nervous system (CNS) (Linás, 2011). Each climbing fibre contacts multiple Purkinje cells, but every cell is receiving inputs only from one fibre.

### 1.3 Cerebellar microcircuit

The cerebellum has remarkably uniform cytoarchitecture, consisting of microcircuits, the basic functional unit of the cerebellum. Microcircuits consist of a microzone of cerebellar cortex and its associated deep cerebellar or vestibular nuclei (Ito, 2013). Each microcircuit represents an individual functional unit however, several microcircuits can be reassembled into multizonal microcomplexes (Apps & Garwicz, 2005). These microcomplexes are made of several microcircuits, all of them being connected to the same group of DCN and inferior olivary neurons.

The functional organization of cerebellar microcircuits can be described as follows (D'Angelo, 2018): Mossy fibres activate Golgi cells and granule cells in the granular layer. Granule cells subsequently process this input and activate all the other cells in the cerebellar cortex via their parallel fibres. Since Golgi cells are receiving excitatory inputs from both parallel fibres and mossy fibres, they are thought to provide inhibitory feedback to the granule cells. In the molecular layer parallel fibres activate Purkinje neurons together with stellate and basket cells which provide inhibitory feedback to Purkinje neurons. Purkinje neurons are also innervated by climbing fibres and after integrating all the incoming inputs, they project their output to the DCN.



## 1.4 Cerebro-cerebellar closed loops

After microcomplexes process the inputs they receive, they project back to the cerebral cortex. The cerebellum communicates with the cerebral cortex via two primary pathways: the efferent, "feedback" cerebello-thalamo-cortical (CTC) pathway and the afferent, "feedforward" cortico-ponto-cerebellar (CPC) pathway (Baumann et al., 2015; Ramnani et al., 2006). These cerebro-cerebellar pathways are contralateral to each other.

The CPC pathway originates in the cerebral cortex, descending through the ipsilateral cerebellar peduncle, establishing synapses in the anterior pontine nuclei (APN), and finally crossing through the contralateral middle cerebellar peduncle to reach the cerebellar cortex.

Animal models have demonstrated that the CPC pathway receives projections from various cortical regions, including the reticular formation, which is involved in autonomic responses (Noda et al., 1990); the posterior parietal associative cortices (Schmahmann, 1996; Schmahmann & Pandya, 1989); the prefrontal executive areas (Schmahmann & Pandya, 1997); the cingulate gyrus (Vilensky & Hoesen, 1981); and the hippocampus (Snider & Maiti, 1976). Additionally, the CPC pathway has bidirectional connections with brainstem neuromodulatory systems involved in mood regulation (Dempsey et al., 1983; Marcinkiewicz et al., 1989). Notably, more than 80% of the fiber tracts in the APN, that connect the cerebrum to the cerebellum, are established between the cerebellum and associative cortical areas, underscoring the cerebellum's significant role in cognitive processes (Palesi et al., 2015). From the pontine nuclei, these inputs are relayed to the cerebellar cortex via the mossy fiber pathway (Schmahmann, 2001).

The CTC pathway originates in the deep cerebellar nuclei, passes through the superior cerebellar peduncle, and is relayed back to contralateral cerebral cortical areas via contralateral thalamic nuclei (Schmahmann, 2001). This pathway enables the cerebellum to establish a feedback loop with the same cortical areas from which it receives input, thus creating *closed cerebro-cerebellar loops* (Middleton & Strick, 2001; Schmahmann, 1991, 1996). While the majority of these loops are closed, some evidence suggests that certain cerebro-cerebellar connections may be more open-ended, wherein a single cerebellar lobule receives projections from multiple cerebral areas (Suzuki et al., 2012).

Nevertheless, our focus will be on the closed cerebro-cerebellar loops, as they form the foundation of major contemporary theories of cerebellar function.

These closed loops serve as the neurobiological substrate for the cerebellum's role in both motor and cognitive processes (D'Angelo 2018; D'Angelo et al., 2016a).

Another critical aspect of these closed cerebro-cerebellar connections is their precise mapping onto the rostro-caudal anatomical distinctions within the cerebellar cortex (vermal, paravermal, and lateral regions) and their corresponding deep cerebellar nuclei (D'Angelo et al., 2016a). These recurrent loops are organized in such a way, that specific regions of the cerebellar hemispheres are bidirectionally connected with distinct areas of the cerebral cortex (Middleton & Strick, 2001). As a result, these closed cerebro-cerebellar loops are highly segregated (D'Angelo, 2018), with each cortical area terminating its projections in a designated region of the pontine nuclei (Schmahmann, 2001).

## 2 The cerebellum and movement

As mentioned in the introduction, the classical view of the cerebellum centres on its role in motor functions. The cerebellum is indeed crucial for the execution of coordinated movements, postural adjustments, balance maintenance, and the acquisition of novel motor skills (Cerminara et al., 2015). A prime example of cerebellar motor function can be illustrated by the finger-to-nose test, a procedure frequently employed in clinical settings (Fugl-Meyer et al., 1975; Swaine & Sullivan, 1993). In this test, the patient begins with their hand positioned alongside the body and is instructed to touch their nose. When the cerebellum is functioning normally, it calculates the optimal trajectory for the movement using visual and proprioceptive information, allowing the patient to move their finger to their nose in almost a straight line. However, following a cerebellar lesion or damage to the cerebellar white matter, the arm's trajectory becomes irregular, with noticeable deviations—a classic example of ataxic movement.

Thus, we will begin our exploration of the cerebellum's contributions to movement by examining the motor consequences of cerebellar dysfunction.

### 2.1 Cerebellar motor syndrome

Diseases or lesions affecting the cerebellum typically result in cerebellar motor syndrome (CMS), characterized by impairments in gait (ataxia), extremity coordination (dysmetria), disordered eye movements, poor articulation (dysarthria), impaired swallowing (dysphagia), and tremor (Schmahmann, 2004).

Limb ataxia refers to uncoordinated movements of the limbs, characterized by difficulties in the precise control of force and timing (Grimaldi, 2013). In the initial stages of cerebellar degenerative disorders, patients typically exhibit poor balance, often struggling to stand on one leg. As the condition advances, locomotion becomes increasingly impaired, leading to a widened gait and challenges with turning, which can result in falls. In more severe stages, walking may require assistance or significant effort. Hypotonia, characterized by reduced resistance to passive limb movement, is particularly common during the acute phase (Grimaldi, 2013).

Dysmetria involves errors in movement trajectory and inaccuracies due to disturbances in the rate, range, and force of movements (Grimaldi, 2013). It typically affects both proximal and distal joints and is often accompanied by corrective movements (Hore et al., 1991). Dysmetria is also evident in dysdiadochokinesis (the impairment of alternating movements), dysrhythmic tapping of the feet or hands, decomposition of movement when attempting to draw an imaginary circle, and proximal overshoot during finger-to-nose testing. Muscle tone is decreased, and titubation—a tremor of the head and trunk—may occur (Grimaldi, 2013).

Tremor is another classic symptom of the CMS. It primarily consists of low-frequency oscillations, with most cases presenting tremor ipsilaterally to the lesion; however, it can also occur bilaterally (Grimaldi, 2013). The most commonly observed tremor in CMS is action tremor, which occurs during voluntary muscle contractions. This includes kinetic tremor, postural tremor, and isometric tremor (Grimaldi & Manto, 2008).

Kinetic tremor arises during the execution of movement, becoming most noticeable as the limb nears its target. Postural tremor occurs when maintaining a posture. Isometric tremor involves involuntary oscillations of one or more body parts during isometric muscle contractions against a fixed resistance, such as when pressing a hand against a table.

Abnormal eye movements include microsaccades, square wave jerks, and erratic eye motions. Normal saccades are slow, oculokinetic nystagmus is abnormal, and patients are unable to inhibit the vestibulo-ocular reflex. Speech is slow, irregular, and with inappropriate volume. Tremor of the voice and ataxic respiration might be also present.

### 2.1.1 Spinocerebellar ataxia

Spinocerebellar ataxias (SCA) are autosomally dominant heterogenous group of neurodegenerative disorders which share clinical features of ataxia (Sullivan et al., 2019), and has attracted much attention of researchers. These symptoms result from the progressive degeneration of the cerebellum, although other brainstem structures are also affected. While there are many types of SCA, they can be categorized based on their pathogenesis (Margolis, 2002). Epidemiological studies indicate a population prevalence of 3 in 100,000 (Ruano et al., 2014), although regional variations exist, the SCA3 is the most common subtype observed worldwide (Sullivan et al., 2019). However, in Cuba, the SCA2 is the most frequent variant, whereas subtype SCA7 being dominant in Venezuela (González-Zaldívar et al., 2015; Paradisi

et al., 2016). Given the similarity of SCA to cerebellar motor syndrome, the primary triad of symptoms includes gait ataxia and incoordination, dysarthria, nystagmus and visual disturbance. SCA may also present with cognitive impairments such as deficits in verbal short-term memory, generalized cognitive decline, frontal-executive dysfunction, or affective dysregulation (Schmahmann, 2004; Sullivan et al., 2019).

## 2.2 Cerebellum as a predictive machine

Many of the movements we perform daily occur too quickly to be corrected based on sensory feedback, such as shooting a goal or playing the piano. Many athletes report that consciously thinking about their movements disrupts their performance (Wolpert et al., 2013).

The inverse engineering of our motor system presents multiple challenges. For instance, consider the example of lifting a glass to one's lips: the input consists of motor commands generated by our motor system, while the desired output is the acceleration of the hand as judged by sensory feedback. This seemingly simple movement depends on numerous variables, such as the position of the arm in space and external factors like the weight of the glass. Given the variety of environmental contexts in which human beings can find themselves, it is remarkable that our nervous system can account for all these factors and compute adequate responses (Wolpert & Kawato, 1998).

The structure of the cerebellum is ideally suited to this role, and it is thought to be the site where predictive *internal models* of our movements are generated. These models simulate the consequences of our intended movements and allow for real-time corrections.

One of the primary postulates regarding brain function is that the brain creates an internal virtual reality. This virtual reality allows the brain to control movements in real time and predict the consequences of intended actions (Llinás & Roy, 2009). This internal representation is generated by our sensory systems. We can conceptualize the motor system in an inverse manner: to move our body, we first generate an internal representation of the movement and then execute it in our environment.

However, this internal representation must be constantly updated to minimize errors and perform movements as precisely as possible (Wolpert et al., 2013). The cerebral cortex requires approximately 100ms to create a conscious representation of the external world. In contrast, the cerebellum operates much faster, with duty cycles of around 10ms (D'Angelo, 2018). This

ability for extremely rapid processing enables near-real-time control of movement, earning the cerebellum the moniker of a “predictive machine” (Ivry, 2000).

In the next sections, we will explain how the cerebellum carries out this crucial role in controlling our body movements.

### 2.2.1 Cerebellar internal models

Fast, coordinated movements cannot rely solely on sensory feedback, as it is biologically too slow (D’Angelo, 2018; Wolpert et al., 1998). It is now well established that the brain addresses this challenge by constructing internal models of reality. There are two types of internal models: **forward and inverse**, with the cerebellar microcircuit serving as the biological substrate for these models (Wolpert et al., 1998; Wolpert & Kawato, 1998).

**Forward internal models** capture the causal relationship between inputs to the system (e.g., the arm) and outputs. Forward models start with the initial condition and “run forward,” predicting future sensory consequences of intended movements based on the motor command (Ito, 2008; Wolpert & Kawato, 1998). This prediction can then be compared with sensory feedback, which is delayed in time from actual movements and corrupted by noise (Diedrichsen et al., 2010). The primary functional output of internal forward models is the prediction of sensory consequences of motor commands (Ito, 2008).

In contrast, **inverse internal models** invert this function, producing a desired motor plan based on initial conditions and contextual features (Wolpert et al., 1998). Inverse models determine the movements required to achieve a desired sensory outcome, taking into account the initial conditions and contextual factors. They are, therefore, well-suited to serve as controllers—the designers of motor plans (Wolpert & Kawato, 1998).

Forward and inverse internal models can be deployed in coordination (Wolpert & Kawato, 1998) and are the result of learning. If each model is accurate, the output of a forward model will match the input of the inverse model (Wolpert et al., 2013).

During development, the CNS acquires an inverse dynamics model of a controlled object, enabling the prediction of outcomes resulting from different muscle contractions (Wolpert et al., 1998). The prediction ability of the cerebellum thus lies in comparing intention

with execution (D'Angelo, 2018). In the next two subchapters, we will review how the cerebellar microcircuit subserves these intricate computations.

### 2.2.2 Inputs of the internal models

Forward models require two inputs: the first from the periphery, updating the state of the model with sensory information, and corollary discharge signals. Corollary discharge (or efference copy) is a copy of the motor plan sent to sensory areas and the cerebellum to predict the sensory consequences of a movement (Sperry, 1950). These signals mimic self-generated sensory information to predict the sensory consequences of our movements. Thus, corollary discharges must be converted from motor to sensory coordinates, a conversion that likely occurs in circuits integrating both motor and sensory pathways. BPN mossy fibers are suitable candidates for this role, as they receive inputs from multiple sensory and motor areas (Leergaard, 2003; Sommer & Wurtz, 2008). Indeed, Huang and colleagues (2013) demonstrated that granule cells receive afferents from BPN, via mossy fibers, carrying motor corollary discharges as well as proprioceptive information channeled via the external cuneate nucleus.

### 2.2.3 Construction and adaptation of the internal models

After granule cells process these inputs, they transmit their outputs to Purkinje cells via parallel fibers. Learning of this information by Purkinje cells is controlled by climbing fibers originating from the inferior olive (Marr, 1969). DCN and inferior olive (IO) form major connections, thus it is useful to consider this system as a whole functional unit (D'Angelo, 2018). Neurons in the DCN, being the main convergence point of Purkinje neurons, are forming GABAergic synapses in the IO, a place of origin of the majority of climbing fiber inputs to cerebellum (Campbell & Armstrong, 1983; Courville & Faraco-Cantin, 1978).

DCN and IO are thus forming a loop, providing a powerful means of the cerebellum to exert control over its own activity. IO neurons produce oscillatory activity (Llinás & Yarom, 1981) and similarly Purkinje neurons which they innervate, also exhibit similar synchronous firing (Bell & Kawasaki, 1972). This synchronous activity was proposed to be crucial for temporal and spatial organization of motor sequences (Welsh & Llinás, 1997). Inhibitory synapses of deep cerebellar nuclei can disrupt symmetry and strength of electrical coupling

between neuronal populations of IO (Lefler et al., 2014), thereby affecting the input of mossy fibres to the Purkinje neurons.

This postulate is central to all cerebellar learning models (D'Angelo et al., 2016b) and asserts that the IO plays an instructive role by conveying error signals via the CF to Purkinje cells. Here, error represents the discrepancy between the intended movement based on instructions and the sensory feedback from the actual movement (Ito, 2013).

Originally, it was thought that CF convey “all-or-nothing” signals (Marr, 1969), encoded in either motor or sensory coordinates, indicating the correct movement in a given context (Marr, 1969). However, nature of such signals is too ambiguous to serve as an instructor in the process of learning (Llinas et al., 1974). Contrary to this hypothesis, it appears that this signal is graded, encoded by pre- and post-synaptic modulation (Najafi & Medina, 2013). The key to unravelling this problem may lie in the synchronous neural activity of IO neurons. Input signaling of an error in movement could be encoded by the activity of specific CF, while the graded information about the error size can be encoded by the number of simultaneously activated CF, thus providing parametric information unavailable through binary coding (Najafi & Medina, 2013). This has been supported by finding that synchronous activity of CF populations can be modulated by sensory information (Wise et al., 2010). CF input might thus provide an instructive signal to Purkinje cells about the correction of movements. Indeed, CF are capable of inducing various forms of plasticity in Purkinje cells (Ito & Kano, 1982; Ohtsuki & Hirano, 2008; Mittmann & Häusser, 2007).

Converging evidence suggests that nucleo-olivary cells play a role in associative learning by regulating inputs from the IO, which transmit prediction errors from unconditioned stimuli to the cerebellum (Najac & Raman, 2015).

#### 2.2.4 Evidence for internal models

There is substantial evidence that the CNS employs such internal models. One classic example is the compensation of grip force (Johansson & Cole, 1992). In this experiment, participants were instructed to hold an object in their hand while elastic loads were applied to the arm. Participants were able to compensate for slippage by adjusting their grip force. Remarkably, this occurred without delay, ruling out the possibility of using sensory feedback from the hands or fingers. This lack of delay implies that the CNS constructs an internal model that predicts the hand's trajectory to determine the appropriate grip force.



Another compelling demonstration was provided by Shadmehr and Mussa-Ivaldi (1994) with the standard force field adaptation paradigm. In this paradigm, participants were instructed to move their hands from one point to another while a robotic manipulandum applied external force to their arms. Interestingly, participants learned to compensate for the perturbations, which initially caused improbable trajectories and endpoint errors. When the external perturbation was removed, participants made similar errors in their movements, but in the opposite direction of the previously applied force. This constitutes crucial evidence that the CNS had adjusted the internal model of the arm, possibly an inverse internal model, which had to be readjusted after the external force became absent.

Additional evidence for this role of the cerebellum provides literature on saccadic eye movements. Saccades are extremely fast, lasting less than 80ms, making sensory feedback too slow to guide the eyes to the target (Keller & Robinson, 1971). The brain solves this problem, by sending the efference copy of the motor command from the cerebral cortex to the cerebellum, which in turn generates an internal feedback signal (Shadmehr et al., 2010). In support of this hypothesis, lesions in the vermis impaired participant's ability to adapt their saccade amplitude in a series of repetitive stereotypical saccades (Golla et al., 2008).

Converging evidence points towards cerebellar internal models in movements but also in cognitive processes. Thus, we proceed to next section of our thesis exploring cerebellum outside of motor domain.

## 3 The new perspective on the cerebellum

Idea that cerebellum might be involved in non-motor functions is relatively new and we have seen a substantial increase of papers concerning the cognitive cerebellum since the 1990s (Adamaszek et al., 2017). We will start our examination of the cognitive functions of the cerebellum with the seminal paper of Schmahmann & Sherman (1998), which is considered a starting point of a broad interest in non-motor functions of the cerebellum.

### 3.1 The Cerebellar Cognitive Affective Syndrome

Schmahmann & Sherman (1998) examined 20 patients with damage of the cerebellum caused either by stroke, postinfectious cerebellitis, cerebellar cortical atrophies or excision of a midline tumour. Using neurological examinations, bedside tests and neuropsychological examination, they described cognitive and emotional symptoms following lesion in the cerebellum, creating a new clinical entity, the cerebellar cognitive affective syndrome (CCAS).

They identified and grouped these impairments into 4 main categories:

- 1) Disturbances of executive functions including deficits in planning, shifting, abstract reasoning, working memory and decreased verbal fluency.
- 2) Impaired spatial cognition including visuo-spatial disorganization and impaired visuo-spatial memory.
- 3) Personality changes manifested as blunted affect and disinhibited behaviour.
- 4) Linguistic difficulties including dysprosodia, agrammatism and anomia.

These clinically significant behavioral changes were apparent during examinations, observed by both family members and medical staff, and could not be attributed to motor control deficits. Symptoms were more pronounced in patients in the acute phase, those with bilateral damage, or those with large unilateral lesions.

Posterior regions of the cerebellum seemed to be particularly important in generating cognitive symptoms of the syndrome, whereas damage to vermis produced pronounced affective symptoms. These affective symptoms were mainly manifested as a blunted affect and disinhibition of behaviour expressed as overfamiliarity, reckless and impulsive actions, and inappropriate comments. Following large infarction adjacent to posterior inferior cerebellar

artery, surgical excision of vermis or paravermal areas, the behaviour of these patients regressed and appeared inadequate of their age.

**Lesions of anterior lobe seem to be less important in generation of these cognitive and affective symptoms.**

One particularly interesting example of the symptomatology of the CCAS was a 22-year-old student who was diagnosed with a midline cerebellar tumour (ganglioglioma) following an accident, which was subsequently resected. After the operation, hospital staff and family immediately noted her blunted affect and personality changes. Her behaviour became disinhibited, and she started undressing in the corridors of the hospital. Nine days after the operation she underwent neuropsychological examination, during which she was hiding her face behind the blankets and acted uncooperatively. Her speech was quick, incomprehensible, and she was speaking in a high-pitched voice, similarly to baby talk. Her IQ was remarkably lower than expected, based on her education, with her verbal IQ in the borderline territory and performance IQ in the mentally deficient range. Global cognitive impairments were manifested in areas of abstract reasoning, calculation skills or planning, which were particularly poor, corresponding to the level of an 8 years old, indicated by her performance on the Maze task. Significant deficits were found in the domain of visual memory, whereas verbal memory was within the normal range. These various impairments eventually resolved and after 2 years from the surgery she continued her university studies.

Other important deficits followed by cerebellar lesions described by Schmahmann and Sherman in their paper were impaired performance on go-no go task and Wisconsin card sorting task, slowness of thinking, inability to concentrate, impairments in visual synthesis of information, complex problem solving, telegraphic speech, acquirement of foreign accent and unusual inflections.

Before the CCAS was recognized, deficits such as decreased arousal and alertness, aphasia and agnosia were classically associated with damage solely to cortical areas. The CCAS can be also distinguished from subcortical syndromes, since it is associated with complex symptoms such as impairment in executive functioning, spatial, linguistic or affective functions.

With more than twenty years after the publication of this revolutionary paper, our understanding of the cerebellum has advanced considerably. In the next two sections we will describe two of the most influential theories of cerebellar functioning.

## 3.2 Cerebellum as a sequencing machine

Cerebellum as a predictive machine, whose role extend beyond motor control might be specialized in the representation of temporal relationships between events and their prediction (Ivry, 2000). The cerebellar general contribution to brain functioning thus might reside in comparing the actual input and prediction and testing for discrepancies. If such discrepancies do not occur, and input is congruent with the predicted event, the cerebellar output is minimal. However, if the prediction is not fulfilled, the cerebellar activity increases and via the bidirectional pathways changes the excitability of the cerebral cortex (Leggio et al., 2011), as it has been shown that the cerebellum is able to modulate activity of the cerebral cortex (Lazzaro et al., 1995; Middleton & Strick, 2001).

*Sequence detection theory* proposes that the cerebellum serves as a detector of change and deviation of sequential events, and the scope of this role extends beyond the motor domain (Leggio et al., 2011; Molinari et al., 2008). Anticipation and prediction by our brain can be achieved by employing feed forward control to identify patterns within incoming information. The cerebellum thus might serve as a device for detection of sequences across virtually all domains (Molinari et al., 2008). This has been demonstrated among others in the somatosensory system, where the cerebellar activity was increased when random omissions in an otherwise regular train of events was presented to participants. On the other hand, the activity in the somatosensory cortex remained closely linked to the presentation of the stimuli itself (Teschke & Karhu, 2000). The cerebellum might be comparing expectations and actual inputs, detecting discordances, to establish more accurate predictions. If the incoming stimulus matches the prediction, cerebellar output is minimal, if a discrepancy is detected, cerebellar afferents are increasing excitability of large portion of cortical areas as a function of better preparedness to react (Molinari et al., 2008).

Cerebellar lesions alter the activity of cortical descending motor pathways (Lazzaro et al., 1995) as it has been observed that the motor cortex showed an increased threshold of excitability in patients who presented with lesions within the contralateral cerebellar hemisphere (Di Lazzaro et al., 1994). Thus, we can infer that the cerebellum has a facilitatory effect on contralateral cerebral cortex.

The cerebellum is involved in the integration of sensory inputs from various modalities, coordinating the brain's acquisition of sensory data (Bower & Parsons, 2003). This was supported by animal studies, when hemocerebellectomy in rats impaired the enhancement of corticomotor response. This type of short-term plasticity was previously ascribed only to sensorimotor cortex (Luft et al., 2002). The cerebellum thus constitutes a link between somatosensory and motor cortices by mediating somatosensory influences on the primary motor cortex (M1), through its cerebello-M1 circuitry.

Other hypotheses suggests that the cerebellar output directly influences the somatosensory cortex (Molinari et al., 2008). The CPC pathway, being one of the largest in the mammalian brain (Tomasch, 1969), originates in the cerebral cortex and reaches almost all regions of the cerebellum. Somatosensory cortex (S1) represents different body parts continuously, with adjacent body parts represented in adjacent regions of the S1 (Merzenich et al., 1981; Welker, 1971). This somatotopic representation, however is not mirrored in the cerebellar granule cells, where it is highly discontinuous and fractured, with different body parts typically mapping onto multiple cerebellar locations (Shambes et al., 1978). This transition from continuous to fractured occurs in the pontine nuclei, which appears to contain several representations of the S1, representing the continuous somatotopic organization (Leergaard, 2003). It is thought that the structural base for comparisons of sequences are embedded in the interactions between mossy and climbing fibres (Ito, 2005).

However, this function of the cerebellum is not limited to the somatosensory domain. In the cognitive task requiring the reconstruction of a sequence of drawings, cerebellar patients performed worse than controls across multiple domains including verbal, spatial and behavioural sequencing (Leggio et al., 2008). Further examination showed that the performance of patients differed depending on their lesions, which suggests that the left and right hemispheres of the cerebellum are involved in the processing of different domains.

Sequence detection has been proposed to be a prominent part of the feedforward cerebellar control, with the detection of a sequences being a prerequisite for prediction, since the successive elements in the sequence can be predicted (Molinari et al., 2008). It is thus hypothesized that the initial role of the cerebellum in predicting sensory consequences of planned movements have extended during evolution, where cerebellar internal models have been employed for pure mental processes in the form of sequences (Leggio et al., 2011; Leggio & Olivito, 2018).

### 3.3 Dysmetria of thought theory

Cerebellum receives its inputs from various cerebral areas via the feedforward CPC pathway. The feedback CTC pathway subsequently redistributes this information back to the cerebral areas (Schmahmann, 1991). According to Schmahmann (1996) it is useful to consider cerebellar contributions in the cognitive and affective functions in the context of its motor role and the motor deficits which result from its damage. These impairments are characterized by abnormal rate, rhythm and inaccuracies in movements. Intact cerebellar functioning secures appropriate conduct of a plan that was designed prior to, and during the execution of the behaviour itself. Without the cerebellum the behaviour is no longer “smoothed” around a homeostatic baseline. This is what Schmahmann coined the *dysmetria of thought* theory.

This theory has a main 5 postulates describing the contribution of the cerebellum to non-motor functions (Schmahmann, 1996, 2004):

- 1) The projections from the paralimbic and associative cortices are the underpinnings of cerebellar contributions to non-motor functions.
- 2) Behavioural and cognitive functions are topographically organized within the cerebellum.
- 3) Convergence of inputs from different associative regions facilitates cerebellar contribution to supramodal functions.
- 4) **The cerebellar contribution to cognition is more of a *modulation* than *generation* in its nature.**
- 5) **The cerebellum performs the same computations in cognitive and affective functions as it does in sensorimotor system.**

Indeed, as the cerebellar cytoarchitecture is extraordinarily uniform, it has been hypothesized for a long time that it contributes to different processes with the same computations. This is allowed by a distinct connectivity pattern of specific cerebellar regions. As we have described in the previous chapter, the cerebellum is involved in several bidirectional pathways involving connections from the reticular formation (Noda et al., 1990), posterior parietal associative cortices, (Schmahmann, 1996; Schmahmann & Pandya, 1989), prefrontal cortices (Schmahmann & Pandya, 1997), cingulate gyrus (Vilensky & Hoesen, 1981), hippocampus (Snider & Maiti, 1976) and also bidirectional connections with the brainstem neuromodulatory systems (Dempsy et al., 1983; Marcinkiewicz et al., 1989). As these loops are highly segregated, it allows the cerebellum to engage in different functions with the same

processes (Kelly & Strick, 2003). This has been referred to as the *universal cerebellar transform* (UCT), when the general function of the cerebellum is the modulation of behaviour, serving as an oscillation dampener, smoothing the behaviour around the homeostatic baseline (Schmahmann, 2004). According to this hypothesis, a universal impairment should follow when the UCT is disrupted. This dysmetria, when it affects the motor domain, is evident in the inability to perform smooth, controlled movements, as can be visible in various symptoms of the cerebellar motor syndrome. Similarly, when dysmetria affects the non-motor functions of the cerebellum, it manifests as various components of Cerebellar Cognitive Affective Syndrome. This condition involves a disconnect between reality and perceived reality, leading to attempts to correct these cognitive and behavioural errors (Schmahmann, 1991, 2004).

It is now widely recognized that the cerebellum's role extends beyond motor control. Lesions in the cerebellum can lead to deficits in executive functioning, abstract reasoning, and language, impacting some of the brain's most complex processes. The cerebellum also plays a crucial role in processing social events, which are fundamental to our daily interactions within society. In the next chapter, we will briefly describe how the brain accomplishes these tasks and continue with a discussion of the connections between the cerebellum and cerebrum, which underlie the cerebellum's contributions to social cognition.

## 4 The social cerebellum

One of the most complex tasks performed by the human brain is navigating our intricate social environment, which complements a hallmark of our species: the ability to engage in large-scale cooperation among unrelated individuals. Although we often take this ability for granted due to the apparent ease with which the brain manages this task, it is an extraordinarily complex process. These processes, collectively known as *social cognition*, appear to involve the cerebellum in a crucial role, as suggested by recent progress in neuroscience.

Brothers (2002) defines social cognition as “the processing of any information which culminates in the accurate perception of the dispositions and intentions of other individuals.” (Brothers, 2002, p. 367). He further describes social cognition as a crucial capacity distinguishing primates from other animals. Social cognition is composed of two fundamental components - emotion recognition and the Theory of Mind (ToM) (Mier et al., 2010).

Emotion recognition refers to the ability to infer another individual's emotional states from externally visible signs, primarily facial expressions, body language, and vocalizations (Mier et al., 2010). It is a bottom-up process, that relies heavily on visual and auditory information, which are first processed by our perception (Schnell et al., 2011).

ToM consists of two levels. The first level, a more primitive, automatic and implicit process also relying on low-level behavioural input, is known as *mirroring* (Coricelli, 2005; Overwalle & Baetens, 2009). The mirror system is thought to simulate observed actions in our motor system, comparing them with our own behavioural repertoire. By matching the observed actions to specific representations in our memory, it enables us to effortlessly infer the intended goal of the observed behaviour (Gallese et al., 2004; Iacoboni et al., 2005; Rizzolatti et al., 1996; Uddin et al., 2007). This simulation is thought to rely on the *mirror neurons* which possess a characteristic property of discharging, not only during the *execution* of goal-directed movement, but also during the *observation* of movement executed by another individual (Gallese et al., 1996; Rizzolatti et al., 1996).

The second level, also known as *mentalizing*, is considered a conscious and relatively demanding, high-level cognitive process of hypothesis testing about the mental state of another person. It underlies inferences of enduring personality traits, social scripts and norms (Amodio & Frith, 2006; Fehlbauer et al., 2022; Overwalle & Baetens, 2009).



Thus, social cognition encompasses both low-level, bottom-up embodied processes and high-level, top-down inferential processes (Ribeiro da Costa et al., 2022). However, these processes are not clearly separable, as the output of one system often serves as input for another (Carr et al., 2003; Jastorff et al., 2015; Van Overwalle, 2009).

As mentioned in the previous chapter, one of the main postulates of the UCT is that the cerebellum performs the same computations, with differences arising solely from varying connections. One of the early perspectives on the cerebellum's role in social cognition proposed that specialized areas within the cerebral cortex were solely responsible for social cognition, while the cerebellum provided domain-general support by engaging non-social functions such as executive functioning, sensorimotor, linguistic, and emotional processing (Overwalle et al., 2014; Stoodley & Schmahmann, 2009). However, the discovery that major networks in the cerebrum involved in social cognition are mapped to distinct areas of the cerebellum has shifted this view, supporting the idea of the cerebellum's direct involvement in social cognition. In the next section, we will explore these networks, how they are projected within the cerebellum and touch on the importance of cerebellum in our evolution.

## 4.1 Functional organization of the cerebellum

Social cognition, like all complex processes, is not confined to specific brain regions but is supported by distributed networks of interconnected areas (Goldman-Rakic, 1988). Networks underlying high-order functions involve association areas in the frontal, temporal, parietal, and cingulate cortices, with each area participating in multiple networks and contributing to high-order information integration (Goldman-Rakic, 1988; Yeo et al., 2011).

The Default mode network (DMN), Salience network (SN) and Executive Control network (ECN) are three key networks implicated in social cognition.

The DMN serves as the neural substrate for internal "self-focused" psychological processes, including reflection on feelings, past experiences, and social interactions (Menon, 2023). It is involved in long-term planning and problem-solving through the retrieval and manipulation of stored conceptual information, often manifesting as mind-wandering.

The DMN is more active during rest than during task performance, allowing us to engage in contemplation of the future and past events, and to solve problems that require extended periods of cognitive computation (Binder et al., 1999; Davey et al., 2016; Menon, 2023; Raichle et al., 2001). This network significantly overlaps with regions such as the medial prefrontal cortex (mPFC) and the temporo-parietal junction (TPJ), which are core areas of mentalizing, suggesting that the DMN, as the brain's physiological baseline, is inherently linked to social cognition (Mars et al., 2012; Schilbach et al., 2008).

The SN functions as a detector, filtering information and identifying stimuli relevant to survival by integrating interoceptive sensations with external cues to guide behaviour (Menon, 2015; Seeley et al., 2007). It operates as a bottom-up affective processing network, while the DMN acts as a top-down mentalizing network (Ribeiro da Costa et al., 2022).

The ECN is most active during demanding cognitive task as it is crucial for goal-directed cognition, managing the retrieval, maintenance, and manipulation of information in the working memory and coordinating activity across other networks (Koechlin & Summerfield, 2007; Petrides, 2005; Seeley et al., 2007). In the literature the ECN is usually divided into left and right ECNs (Bilevicius et al., 2018; Seeley et al., 2007) however, they likely represent a single, homologous network (Habas et al., 2009).

The ECN and DMN are traditionally considered antagonistic, as they are activated or inhibited depending on task engagement. The anterior insula (AI), a core region of the SN, regulates the switch between the DMN and ECN. Upon identifying salient stimuli, the ECN allocates additional attentional resources, with the AI inhibiting DMN activity to prioritize task-related processing (Menon & Uddin, 2010; Sridharan et al., 2008).

One of the most important and revolutionary discoveries was the discovery that majority of the intrinsically connected networks (ICNs), including the SN, DMN and ECN are projected onto homotopic map in the cerebellar cortex (Buckner et al., 2011; Habas, 2021; Habas et al., 2009; O'Reilly et al., 2009; Sang et al., 2012). This map starts in the anterior lobe with an inverted representation, beginning with the primary somatomotor cortex, premotor or somatomotor integration cortex and progressing to the SN, ECN and DMN in the Crus I/II. A second map begins in Crus I/II and forms an upright mirror-image representation that extends through the posterior lobe, ending at hemispheric lobule VIII with the second somatomotor representation. Together, these two maps represent an orderly progression from the somatosensory cortex to the associative cortices (Buckner et al., 2011).

These findings were later confirmed and expanded by functional connectivity studies that also included independent task activation (Guell et al., 2018). These studies revealed two somatomotor representations in the cerebellum, whereas non-motor functions were represented three times (Figure 4 & 5). Working memory, language, social and emotional task processing are all represented threefold in the cerebellum and these resting-state data were congruent with task activations for each function.

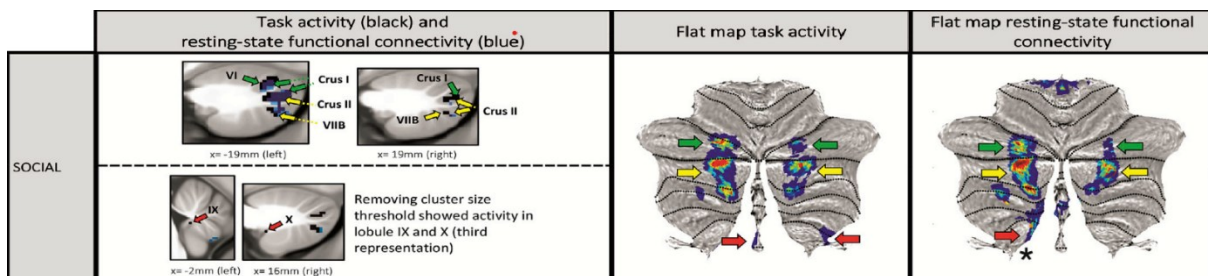


Figure 3. Threefold representation of social processing in cerebellum. First representation is indicated by a green arrow, starts in the lobule VI and continues to Crus I. Second representation, indicated by yellow arrow starts in the Crus II and continues to VIIIB. Red arrow marks the third representation, in the lobules IX and X, only visible after lowering the threshold for activation (Guell et al., 2018).

The cerebellum is traditionally divided into the anterior sensorimotor region and the posterior cognitive region (Schmahmann, 2001; Stoodley & Schmahmann, 2009). However, evidence suggests the existence of a third functional distinction within the cerebellum, specifically dedicated to emotional processing (Habas et al., 2009; Sang et al., 2012). The “limbic cerebellum” (Figure 5) is located in the phylogenetically older regions including the vermis, paravermal areas and the flocculonodular lobe (Schmahmann, 1991).

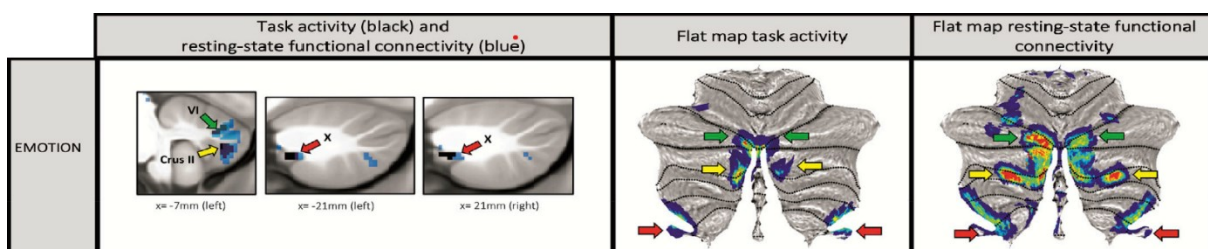


Figure 4. Threefold representation of emotional processing in cerebellum. First representation is indicated by a green arrow, starts in the lobule VI and continues to Crus I. Second representation, indicated by yellow arrow starts in the Crus II and continues to VIIIB. Red arrow marks the third representation (Guell et al., 2018).

These findings suggest that cerebellar lobules are distinct, heterogeneous structures that can be subdivided into functional subregions with different patterns of connectivity. These functional subregions do not adhere to traditional anatomical boundaries but are instead organized along gradients (Guell et al., 2018).

## 4.2 The cerebellar networks

The cerebellum thus maps onto most of the ICNs. Additionally, the extent of cerebellar involvement in a particular cerebral network is generally predicted by the size of that network in the cerebrum, with the majority of the cerebellar cortex being connected to association areas (Buckner et al., 2011).

The posterior cerebellum is a vital part of the SN, ECN and DMN (Figure 6), underlying its more advanced functions compared to the anterior cerebellum. These networks may represent cortico-cerebellar loops as all of them include pontine nuclei (Habas et al., 2009). The pontine nuclei are known to serve as the final relay station for corticopontine fibers before these signals reach their ultimate targets in the cerebellum (Palesi et al., 2015; Schmahmann & Pandya, 1997).

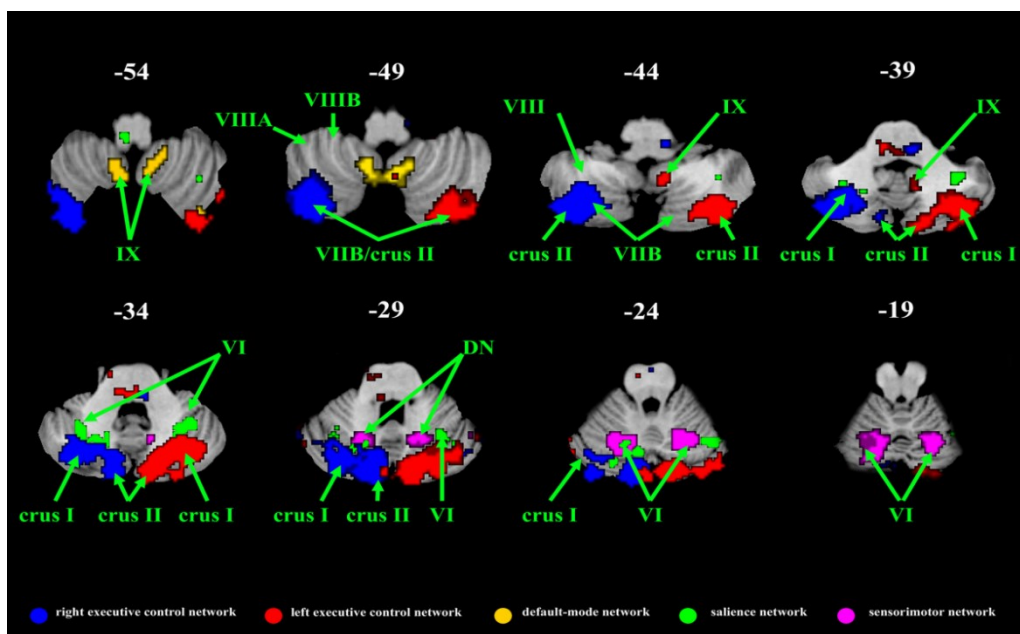


Figure 5. Distinct cerebellar contributions to five intrinsic connectivity networks. All cerebellar clusters are overlaid on the same axial slices. Right and left executive control networks represent a homologous network (Habas et al., 2009).

The most voluminous neocerebellar lobule VII is occupied by the ECN and DMN with a predominance of the ECN (Habas, 2021; Marek et al., 2018). The prominent role of the Crus I/II in cognition has been also previously established by anatomical tracing studies and tractography, revealing their connections with prefrontal and parietal association cortices (Habas & Manto, 2018; Middleton & Strick, 2001; Schmahmann & Pandya, 1989, 1997).

These anatomical observations were confirmed by findings of Crus I/II being functionally coupled to contralateral prefrontal cortex (Krienen & Buckner, 2009; O'Reilly et al., 2009; Sang et al., 2012). Functional neuroimaging in humans have shown that the Crus I is involved in executive functions such as abstract reasoning (Monti et al., 2007), working memory (Chen & Desmond, 2005) and response selection (Desmond & Fiez, 1998). Activation clusters associated with the ECN also extend into lobules VI and VIIB (Habas et al., 2009).

Interestingly, the ECN is overrepresented in the cerebellum, occupying 2.3 times more territory compared to the cerebrum—a phenomenon not observed in other primates. Kelly & Strick (2003) using neurotropic virus tracing revealed a closed-loop circuit in New World capuchin monkeys. encompassing projections from area 46 (equivalent to the dorsolateral PFC in humans), to the cerebellar region Crus II. Ramnani and colleagues (2006), using diffusion tensor imaging (DTI), showed that fibres connecting the prefrontal cortex and cerebellum constitute larger portions of cerebellar peduncle in humans compared to macaque monkeys.

This evidence suggests that different cerebellar areas might have been under different evolutionary pressures (Balsters et al., 2010). The prefrontal cortex is proportionally larger in humans than in other primates, suggesting it has undergone large changes in our evolutionary history compared to posterior frontal motor areas (Passingham, 2002). Balsters and colleagues (2010) demonstrated that cerebellar regions Crus I and Crus II, which are connected to prefrontal areas, have also undergone similar expansion and are larger in humans compared to chimpanzees and capuchin monkeys. Thus, the overrepresentation of the ECN in the human cerebellum might be a crucial neurobiological substrate underlying our cognitive flexibility, distinguishing us from other species (Marek et al., 2018).

Interestingly, clusters of the ECN in lobule VII are surrounding the DMN clusters found in the Crus I/II (Buckner et al., 2011; Habas, 2021). The recent evolutionary expansion of Crus II, with its involvement in both the ECN and DMN, leads to intriguing speculations about the evolution of our species. Archaeological and anthropological evidence suggest that creation of composite tools have fueled the evolution of our large hominid brain (Ambrose, 2001).

The cerebellum, essential for fine, precise movements, plays a crucial role in advanced toolmaking. It was hypothesized that the observational learning, needed for successful transmission of tool-making knowledge, crucially engaged the cerebellum which further fueled the evolution of our cognitive and social cognitive functions (Vandervert et al., 2024).

Other cerebellar clusters showing coherence with the DMN are located in the lobule IX (Buckner et al., 2011; Habas, 2021). The lobule IX has been implicated in various functions, including thirst satiation (Parsons et al., 2000), motor synchronization (Jantzen et al., 2004) or working memory (Desmond & Fiez, 1998). However, most pertinent to its possible function in the DMN is its involvement in elaboration of past and future events (Addis et al., 2007).

The clusters of functional connectivity with the Salience network in the cerebellum are found bilaterally in the lateral and ventral part of the lobule VI and adjacent Crus I with an extension to Crus II (Habas et al., 2009; Sang et al., 2012). Vermal lobule VI and lateral parts of lobules VI/Crus I have been implicated in pain and fear processing, startle reactions or grimacing (Dimitrova et al., 2003). Furthermore, cerebellar strokes in the hemispheres of lobules VII-VIII result in lowered ability of experiencing pleasant feelings in response to happiness evoking stimuli (Turner et al., 2007). The vermal portion of lobule VI establishes reciprocal connections with the hypothalamus via the fastigial nuclei (Azizi et al., 1981; Haines et al., 1997) and has a direct role in interoceptive awareness (Gray et al., 2007).

Topographical organization of the distributed networks in the cerebellum is significantly more variable than in the cerebral cortex (Marek et al., 2018). This variability is also associated with individual mental abilities as coherence between Crus I/II and right ECN is correlated with individual's executive functioning (Reineberg et al., 2015). This highlights the cerebellum's crucial role in cognitive functions and provides indirect evidence of its importance in our evolution. Dunbar's (1998) influential *Social brain hypothesis* states that our brains have expanded throughout evolution due to the challenges posed by our increasingly complex social lives. Survival in this complex environment depends not only on the ability of representing relationships between oneself and members of the group but also on representing the relationships between groupmates themselves (De Waal, 1982), thus creating pressure for the evolution of cognitive functions. The cerebellum's role in social cognition may have been pivotal in the evolution of our brains and modern society (Vandervert et al., 2024). In the next chapter, we will discuss how the cerebellum contributes to the mentalizing and mirroring systems, processes that differentiate us from other primates.

## 5 The mentalizing cerebellum

One of the first meta-analysis focusing solely on cerebellum and mentalizing was the study of Overwalle et al. (2014), involving 350 papers, examining cerebellar involvement in various types of mentalizing ranging from event mentalizing (inference about agent's momentary belief based on given behavioural event description) to more cognitively challenging abstract mentalizing. Abstract mentalizing constitutes tasks when the participant is instructed to infer personality traits during stereotyping of social groups or in the counterfactual thinking – imagining a hypothetical event in the future or past (Van Hoeck et al., 2013). They found a robust activation of the posterior cerebellum in response to mentalizing tasks involving a higher level of abstraction. On the other hand, less demanding mentalizing task did not evoke substantial cerebellar activation.

Overwalle and colleagues (2014), in their interpretation first adapted the domain-general role of the cerebellum in cognitive processes, that the cerebellum contributes to socio-cognitive processes indirectly by employing non-social functions (Stoodley & Schmahmann, 2009).

However, in their later commentary, Van Overwalle et al. (2015a) proposed an alternative explanation of their results, based on the functional connectivity study of Buckner et al. (2011), when they discovered a large overlap between all types of mentalizing concerned in their study and the clusters of the DMN in the Crus I. They also found support for phylogenetically older somatomotor integration network embedded in the anterior cerebellum to be involved in mirroring tasks, resembling role of the motor cortices in the cerebrum (Rizzolatti et al., 1996; Van Overwalle, 2009).

For more cognitively demanding forms of mentalizing, such as abstract mentalizing, the overlapping activation with the DMN in the cerebellum was remarkably consistent, employing not only Crus I but also lobule IX. This substantial overlap implies common underlying processes between the DMN and social cognition, in line with evidence of this overlap in the cerebrum (Mars et al., 2012; Schilbach et al., 2008).

More recent metanalysis, however localized cluster of activation specific to mentalizing in the Crus II (Van Overwalle et al., 2020a). The previously reported activation of the Crus I thus might not be specific to mentalizing but could instead reflect the supportive role of executive functions, as these clusters were located at the border between the ECN and DMN (Buckner et al., 2011). However, Van Overwalle et al. (2020a) in their analysis included only specific

regions of interests (ROI) in the posterior cerebellum, established in previous studies, so it is possible that other cerebellar regions are also involved in mentalizing. Another meta-analysis found evidence that mentalizing engages both Crus I and Crus II equally, although it included only studies focused on mirroring (Guell et al., 2018).

Nevertheless, both ROIs used by Van Overwalle et al. (2020a) are connected with bilateral temporoparietal junction (TPJ) and medial prefrontal cortex (mPFC), creating bidirectional closed cerebro-cerebellar loops (Overwalle & Mariën, 2016; Van Overwalle et al., 2019a). TPJ and mPFC are both crucial regions of the DMN and mentalizing network, where TPJ is mainly responsible for perspective taking and transient mental state inferences about other people such as their goals, desires and beliefs. On the other hand the mPFC subserves the attribution of more enduring traits and qualities about the self and other people as it has been ascribed a general role in reasoning about one's own or others' mental and affective states (Amodio & Frith, 2006; Decety & Lamm, 2007; Van Overwalle, 2009).

In conclusion, this evidence is pointing to a specialized role of the Crus II in mentalizing with a possible contribution of Crus I.

Although the role of Crus I in more complex forms of mentalizing remains unclear, it is implicated in phylogenetically older somatomotor integration and premotor networks within the anterior cerebellum, forming part of the cerebellar mirror system (Overwalle et al., 2014; Van Overwalle et al., 2015a). Interestingly, neurons in the cerebellum exhibit mirror-like activity, being activated both by the observation and execution of actions (Gazzola & Keysers, 2009), supporting the idea that the cerebellum is involved in the mirror network.

Crus I is connected with the superior temporal sulcus (Sokolov et al., 2012a; Sokolov et al., 2012b), which plays a crucial role in the perception of biological movement (Bonda et al., 1996; Puce et al., 1998; Van Overwalle, 2009). The multimodal posterior superior temporal sulcus (pSTS) is responsible for identification of socially relevant cues based on integration from both auditory and visual pathways (Haxby et al., 2000; Pitcher & Ungerleider, 2021; Sellal, 2022). It has been hypothesized to also play a role in later stages, comparing the "mirror code" output of the motor areas with sensory feedback following the observed actions, generating predictions (Iacoboni et al., 2001). Thus, Crus I might contribute to mirroring via interaction with the pSTS.



The cerebellum is functionally organized in anterior/medial-to-posterior/lateral gradient, where the lateral structures are engaged in more complex processing contrary to vermal and paravermal areas.

The medial portion of the lobule VI appears to be involved in early identification of biological movement, as it is sensitive to the “authenticity” of the biological motion similar as the STS or other cortical regions responding to biological motion (Ferrari et al., 2022). When animations depicting biological movements are presented upside-down, the STS is recruited to a lesser degree (Grossman & Blake, 2001). Perception of biological movements is thus orientation dependent, as when it is depicted upright, it appears less natural, contradicting gravity, thus might be harder to recognize (Pavlova, 2012). On the other hand, more lateral Crus I modulates higher-level cortical processing, based on feedback it receives from cortical areas (Ferrari et al., 2022; Van Overwalle et al., 2020b).

These results show that cerebellum contains regions specialized in mentalizing by recruiting *domain-specific* mentalizing processes as a part of the DMN/mentalizing network.

The primary role of the cerebellum is believed to be the generation and updating of internal models used for predictions. For example, within the mirror system, the vermal lobule VI may deploy perceptual internal models to predict visual sequences based on participants' real-world knowledge (Ferrari et al., 2022). However, these internal models are not limited to mirroring alone but also extend to more abstract forms of mentalizing, which will be discussed in the next chapter.

## 5.1 Internal models of social cognition

Previously mentioned analyses of Overwalle and Mariën (2016) and later Van Overwalle et al. (2019a) can shed light on functioning of the cerebro-cerebellar loops in mentalizing by examining the directionality of these connections. The psycho-physiological interaction (PPI) analysis employed by Overwalle & Mariën (2016) allows the testing of the hypothesis that the activity of a brain area (e.g. cerebellar lobule) can be explained by an interaction between the presence of a cognitive task (e.g. socio-cognitive task) and task-related activity in another area of the brain (e.g. cerebral mentalizing network). They have found a pattern of connectivity between the dorsal mPFC and the right TPJ with a cluster located in the posterior cerebellum, together with back propagated connections from the latter to the left TPJ.

Van Overwalle et al. (2019a) using dynamic causal modelling (DCM) that addresses some limitations of PPI replicated and extended their previous results by revealing an ipsilateral functional connectivity of posterior cerebellum and TPJ. Although majority of cerebellar connections with cerebrum are contralateral (70-80%), smaller portion terminate in the ipsilateral regions (Krienen & Buckner, 2009). This finding from functional connectivity is supported also by anatomical studies (Sokolov et al., 2014; Suzuki et al., 2012). In the final model Van Overwalle et al. (2019a) identified bidirectional closed loops with a portion of the Crus II and bilateral TPJ. Within the cerebrum, their model identified unidirectional connections from the bilateral TPJ to the ventral and dorsal mPFC. Furthermore, they identified connections of the cerebellum with the precuneus (PC), another important region of the DMN/mentalizing network, involved in mental imagery and imagination of other's perspective (Cavanna & Trimble, 2006; Ghaem et al., 1997; Hanakawa et al., 2003; Knauff et al., 2003).

Overwalle & Mariën (2016) provide a speculative interpretation of their findings, noting that their results are based on a correlational analysis and cannot establish causal relationships. Output from the right TPJ and PC is forwarded into the posterior cerebellum, where it is integrated with the output from the mPFC. This cerebellar cluster subsequently projects to the left TPJ, which is in turn connected with the dorsal mPFC and right TPJ.

These cerebro-cerebral loops are a biological substrate underlying the computation of internal models in social cognition. As we have seen one of the main postulates of UCT is that the cerebellum performs the same computations with differences arising only due to differences in the connectivity of the cerebellum (Schmahmann, 2004).

The cerebellum might be comparing expectations and actual inputs (Molinari et al., 2008). If a discrepancy between expectations and outcomes are detected, the cerebellum might influence the (de)synchronization of cerebral areas through the thalamus (Habas et al., 2019).

Signals from the cerebellum might continuously monitor social interactions and assess whether they align with the predictions it has generated. This function could be an exaptation of motor internal models, which are based on somatosensory information. In the cognitive domain, the cerebellum is involved in event sequencing (Leggio et al., 2011; Van Overwalle et al., 2020a). Internal models are shaped by error signal when predictions are not fulfilled. Van Overwalle et al. (2019a) found that all connections between the cerebellum and cerebrum were negative, indicating that increased cerebellar activity was associated with decreased cerebral activity, suggesting that the cerebellum emits an error signal that prompts the cerebral cortex to

adjust its activation in the opposite direction. Thus the cerebellum might contribute to social cognition by supporting the TPJ, STS and other structures with detection and signaling of violated predictions and event sequencing, fine tuning the models of social interactions (Van Overwalle et al., 2019b).

For instance, if we move to a new neighbourhood and meet our new neighbour, who appears friendly, we reciprocate this behaviour because our cerebellum predicts that he will continue to act in a similar manner in future interactions. However, if a subsequent interaction reveals signs of intentional aggression, this new information is assessed and processed by the cerebral mentalizing network. The output from this network is then sent to the cerebellum, where it is integrated into the internal model, thereby updating our mental representation of the neighbour.

Furthermore, this hypothesis suggests that the cerebellum's contribution should be relatively minimal during the processing of highly predictable, stereotypical events, but more significant during the reconstruction of past events (such as integrating them into the internal model) or in the process of the prediction itself. This aligns with observations that cerebellar activity is more engaged in tasks requiring higher levels of abstraction (Overwalle et al., 2014; Van Overwalle et al., 2015a).

If these theoretical claims are correct, the cerebellum should be more engaged when a prediction of the sequences of social events is necessary for successfully inferring mental states (Van Overwalle et al., 2020a). Van Overwalle et al. (2019c) developed a task aimed at examining this hypothesis of the sequencing ability of the social cerebellum. Participants are shown four cartoon-like pictures depicting an event. They are instructed to organize this sequence in a correct temporal order. The cartoons can either depict mechanical events (car crash), social scripts (going to grocery store), false belief or as extended in Heleven et al. (2019) true belief.

False belief is one of the most frequently used tests of mentalizing in children. The classic version involves two characters, Sally and Anne, represented as dolls (Wimmer & Perner, 1983). Sally places an object in Box A and then leaves the room. While Sally is away, Anne moves the object from Box A to Box B. Children are then asked where Sally will look for the object when she returns. To answer correctly, children must understand that Sally holds a false belief, expecting the object to be in Box A because she did not see Anne move it. This task requires children to grasp that Sally's knowledge of the world differs from their own.

The involvement of the TPJ, which is connected to the cerebellum, is crucial in this task as it plays a key role in perspective-taking (Schurz et al., 2013).

In contrast, the true belief task involves a protagonist whose mental state is consistent with reality. In the true belief version of the Sally-Anne task, Sally places the object in Box A, and when she returns, the object is still in Box A, making Sally's belief align with reality. Unlike the false belief task, this version requires fewer inferential processes. Heleven et al. (2019) also included verbal version of the task.

Their results revealed that, compared to a control condition, that did not involve sequencing, all types of stories elicited cerebellar activity, whether or not they were social in nature. This supports the general role of the cerebellum in sequencing. Furthermore, the results further support the hypothesis, that specific regions of the posterior cerebellum are activated in reconstructing sequences of social actions. Crus I/II were preferentially activated by organizing novel sequences involving mental state attributions in comparison with routine action sequences, either with or without a social element. Specifically, all predicted comparisons between false belief and mechanical events were significant, supporting the general involvement of cerebellum in prediction and error correction of sequences. At the same time Crus I/II were specifically activated by sequences involving false and true belief.

Thus, converging evidence points to the function of the cerebellum in the construction of predictions based on internal models, not only in the motor but also in the social domain.

The importance of the “social cerebellum” is also emphasized in the clinical perspective, as the converging evidence points to the importance of cerebellar internal models in Autism spectrum disorder (ASD), which can be conceptualized as a disorder of prediction (Sinha et al., 2014).

## 5.2 Cerebellum and autism

ASD is a neurodevelopmental disorder which is characterized by a triad of symptoms: atypical social behaviour, deficits in communication and the presence of repetitive and inflexible behaviours (American Psychiatric Association, 2013). Research indicates that people with ASD show altered structural features of the cerebellum with reduced cerebellar volume, particularly in regions associated with cognitive and affective functions such as Crus I/II and posterior vermis (D'Mello et al., 2015; Stoodley, 2014). Postmortem studies demonstrate

reductions in the number of Purkinje cells and their reduced size (Fatemi et al., 2002; Whitney et al., 2008). Additionally, genetically engineered mice, with alterations in Purkinje cell morphology are show altered social “autism-like” behaviour (Tsai et al., 2012). Functional imaging has revealed decreased activation of Crus I during mentalizing tasks in individuals with autism (Kana et al., 2015). Furthermore, individuals with ASD show altered functional connectivity of the cerebellum with the cerebral mentalizing network (D’Mello & Stoodley, 2015; Igelström et al., 2017), with animal models confirming the importance of cerebro-cerebellar loops in autism-like behaviour (Kelly et al., 2020).

Overall, the cerebellum is one of the most consistently reported sites of abnormalities in ASD (D’Mello & Stoodley, 2015; Kelly et al., 2020; Stoodley, 2016).

Given that the cerebellum’s main contribution to brain function lies in its predictive capabilities, which enable adaptive and flexible behaviour, it is possible that the abnormality of cerebellar functioning could be the underlying pathological mechanism in autism (Stoodley, 2016; Stoodley & Tsai, 2021). A prominent example of this are the difficulties in mentalizing which are thought to be primary contributors to the social functioning challenges faced by individuals with ASD (Baron-Cohen et al., 1985). Mentalizing tasks used to measure this ability are inherently dependent on the ability of making predictions about mental states of others based on current observations (Baron-Cohen et al., 1985; Sinha et al., 2014).

However, impairment in predictive abilities is not limited to the social domain. The high prevalence of sensory hypersensitivities in ASD is also consistent with impaired predictive abilities (Leekam et al., 2007; Sinha et al., 2014), as the predictability of stimuli is correlated with the habituation to non-salient stimuli (Herry et al., 2007). This impaired ability of prediction also contributes to behavioural rigidity and cognitive inflexibility, which are other characteristic features of ASD (Stoodley & Tsai, 2021).

Disrupted cerebellar functioning during development may therefore lead to failure in acquiring and automatizing information necessary for sensory habituation, normal social interactions, and cognitive flexibility, positioning the cerebellum as a key region in ASD pathology (Stoodley, 2016).

Importantly, dysfunction of the cerebellum can also explain several emotional problems observed in ASD (Stoodley & Tsai, 2021). Therefore, in the last chapter of our thesis we will discuss cerebellar contributions to the processing of affective stimuli, which is also the main focus of our thesis.

## 6 The emotional cerebellum

As previously discussed, the limbic emotional cerebellum likely encompasses several specific and non-specific regions, primarily located in the vermal and paravermal areas (Sang et al., 2012; Schmahmann, 1991; Snow et al., 2014), also implicated in autonomic functions. Vermis, together with lateral hemispheres, of the posterior cerebellum is anatomically connected with brain stem reticular nuclei (Dietrichs & Walberg, 1979) and hypothalamus (Haines et al., 1997). These connections are pivotal for emotional experience, as these structures are responsible for evaluating the emotional significance of stimuli and subsequently modulating autonomic, chemical, and behavioural responses (Barrett et al., 2007).

Posterior vermal and paravermal areas with its associated DCN, with a prominent role of lobule VI-VII are involved in processing of *primary emotions* (Adamaszek et al., 2017). Anger, fear, disgust, sadness and happiness are considered primary emotions, as they are common across different species and cultures (Ekman, 1992). As shown by Baumann & Mattingley (2012), each emotion is subserved by specific loci, mainly in the vermal and paravermal regions, with some degree of overlap, such as fear and anger sharing common activation of right vermal lobule VIIIA (Baumann & Mattingley, 2012).

Another intriguing overlap was observed in the vermal lobule IX, which was activated during both anger and disgust. Notably, the vermal portion of lobule IX (see Figure 6) has been identified as part of the DMN (Buckner et al., 2011; Guell et al., 2018). Although prototypically these two emotions are distinct, in humans, they involve wider socio-cultural implications. Anger and disgust are key components of moral processing, often arising when one's values and beliefs are challenged (Rozin et al., 2008; Rozin & Fallon, 1987). This is an interesting implication as the DMN plays a crucial role in self-related processes, where social identity, along with values and beliefs, is integral to the construction of the self (Decety & Chaminade, 2003; Rochat & Striano, 2002).

In conjunction with clinical data showing that lesions in the vermal and paravermal regions often lead to pronounced affective symptoms (Schmahmann & Sherman, 1998), this converging evidence supports the significant role of the cerebellum in emotional processing.

## 6.1 Predominance of negative emotions

Although cerebellum is engaged in processing of emotions regardless of their valence, a predominance of negative emotions has been suggested (Adamaszek et al., 2017). For instance, Schraa-Tam et al. (2012) showed that negative emotions evoke strong activation in lateral lobules VI and VII and vermal VIII and IX, whereas positive emotions evoke only mild activation of Crus II. Another fMRI study showed activation of the cerebellum exclusively to anger (Park et al., 2010).

Contrary to this proposed negative bias of the cerebellum, an fMRI study of Peelen et al. (2007) reported a cluster of activation in the cerebellum responding only to positive emotions.

One of the explanations of this conflicting results is that positive and negative emotions are processed within different circuits. Appreciation of a positive emotions involves more sophisticated processing, including reflections of the self thus, employing phylogenetically younger circuits including the prefrontal cortex and the cortical executive system (Paradiso et al., 1999). In line with this hypothesis, positive emotions evoke only mild activation in the cognitive Crus II, in opposite to robust activation of multiple cerebellar regions by negative emotions (Schraa-Tam et al., 2012).

On the other hand, negatively valenced emotions have a deep important meaning in our evolutionary past, thus are processed by phylogenetically older circuits including vermal and paravermal areas of the cerebellum. Negative emotions constitute highly salient stimuli and their preferential processing might have been favoured by the evolution (Öhman et al., 2001). For example, the emotional expression of anger is signaling, that an attack might be inbound, and the recipient needs to be prepared to defend themselves. The cerebellum seems to be predominantly activated by stimuli indicating a potential danger in our environment (Schraa-Tam et al., 2012). The cerebellum might be involved in prediction of these events and subsequently engaged in preparatory mechanisms. This defense lies in triggering of the preparatory mechanisms known as the flight-or-flight response, causing autonomic changes in organisms which are mediated by distinct hypothalamic nuclei, with stimulation of the hypothalamus evoking defensive aggression (Siegel et al., 1999). It has been hypothesized that the flight-or-flight responses involve cerebello-hypothalamic connections (Adamaszek et al., 2017). Furthermore, the cerebellum is connected with the amygdala (Turner et al., 2007), which is a crucial structure implicated in fear and detection of threat invoking stimuli (LaBar &

LeDoux, 1996). Moreover, the amygdala has been shown to modulate the expression of aggressive behaviour in hypothalamus (Siegel et al., 1999).

The cerebellar vermis might thus be directly involved in recognition of emotional stimuli and the subsequent facilitation of defensive mechanisms, whereas the cerebellar hemispheres might contribute to more cognitive elaborations required by positive emotions. Crus I/II are part of the executive cognitive cerebellum, recruited by cognitive aspects of emotional processing including working memory, allocation of attentional resources, emotion evaluation or response selection (Adamaszek et al., 2017).

Thus, the processing of distinct dimensions of emotions in the cerebellum appears to be functionally segregated (Colibazzi et al., 2010; Styliadis et al., 2015). Circumplex Model of Affect (Russell, 1980) conceptualize emotions along two independent dimensions: valence and arousal. Each of these two dimensions are processed in distinct cortical neural circuits regardless of their sensory domain (Adolphs, 2002; Anderson et al., 2003; Lewis et al., 2007), which appears to be the case for the cerebellum as well.

This segregation can be explained by differences in connectivity within cerebellar lobules between structures such as the amygdala and hypothalamus (Schmahmann, 2000; Strick et al., 2009) which are both points of convergence of inputs from the limbic system (Beauregard et al., 2001). Distinct nuclei of amygdala have been implicated in different aspects of valence and arousal processing (Styliadis et al., 2014) and have different patterns of connectivity with vermal and hemispheric cerebellar lobules (Roy et al., 2009). Additionally the mPFC, implicated in cognitive evaluation of affective stimuli and emotion regulation (Etkin et al., 2011), is functionally connected with the Crus I (Krienen & Buckner, 2009).

Using a magnetoencephalography (MEG), Styliadis et al. (2015) demonstrated that the valence and arousal are processed in parallel and relatively independently in distinct cerebellar lobules. These findings align with the parallel distributed model of emotional processing (Barrett et al., 2007) and the more recent Conceptual act theory of emotions (Lindquist et al., 2012; Lindquist & Barrett, 2012), both of which are related to the Circumplex Model.

In contrast to the Basic Emotions Theory, which assumes the existence of a limited set of emotions that are universal across all cultures, biologically inherited and associated with distinct pattern of physiological activations (Ekman, 1992), these models propose that multiple brain circuits process distinct inputs in parallel. In this view, emotions are emergent phenomena,



not governed by localized processing but arising from distributed activity across large-scale brain networks.

The conceptual act theory of emotions (Barrett, 2009; Barrett et al., 2007; Lindquist et al., 2012; Lindquist & Barrett, 2012) posits that emotions are constructed through interactions among domain-general networks, whose primary functions are not specifically affective. Emotions arise from distinct patterns of coactivation across these networks, meaning that no single brain region is specific to one emotion; rather, one region is coactivated by multiple emotions. This theory is supported by neuroimaging studies, which have shown that specific emotions do not activate isolated brain circuits but instead involve overlapping activation across a large network. This network has been coined the General Emotion Network (GEN) and it constitutes a substantial overlap with the DMN and SN (Jastorff et al., 2015; Lindquist et al., 2012). Emotion processing also engages the mirror system, which interacts with the GEN. In this framework, perceptual inputs are initially processed within the mirror system and then integrated into emotion perception, possibly via the right anterior insula, which exhibits strong functional connectivity with both networks (Jastorff et al., 2015). According to this theory, multiple features of emotional experience are parallelly constructed in different brain networks.

Similarly in the cerebellum, the processing of valence, arousal and their interaction seems to unroll in parallel and in distinct cerebellar lobules (Styliadis et al., 2015). Furthermore, this processing seems to be hierarchically organized in the temporal domain, with processing priority of high arousal stimuli followed by unpleasant and later pleasant valence by high arousal interaction, confirming the hypothesis that negative emotions are prioritized in processing (Schraa-Tam et al., 2012). Arousal processing was identified within a time window of 160ms, while valence processing began at 420ms. Interestingly, in the cerebrum, valence processing is resolved first at 100ms, followed by arousal at 200ms (Olofsson et al., 2008). This suggests an inverted temporal processing pattern in the cerebellum, where information about arousal is extracted before information about valence (Styliadis et al., 2015).

The cerebellum is thus engaged in fast processing of high arousal and unpleasant stimuli with slower processing of pleasant and low arousing stimuli.

The prioritization of negative stimuli is likely due to its importance for individual fitness (Öhman et al., 2001). The activity related to high arousing stimuli was located within vermal lobules VI and VIIIa. Furthermore, the activation associated with unpleasant stimuli was located in the left lobule VI, while pleasant stimuli did not elicit significant activity, consistent

with findings implying a preference for processing of negative emotions in the cerebellum (Ferrucci et al., 2012; Schraa-Tam et al., 2012). Interestingly, interaction between valence and arousal, namely highly arousing pleasant stimuli elicited activation in the hemispheric lobule V and Crus I. This suggests that the cerebellum is a place of an integrative process between these emotional and attentional dimensions and supports the hypothesis that processing of different emotional dimensions are segregated in the cerebellum.

## 6.2 Implicit and explicit processing of emotions

Moreover, affective processing seems to employ implicit and explicit pathways (Shobe, 2014; Scheuerecker et al., 2007), with the cerebellum being implicated in both (Adamaszek et al., 2017). Ferrucci et al. (2012) and Schutter & van Honk (2009) showed that neurostimulation can enhance processing of emotions, with no effect on the self-reported mood of participants. This suggests that neurostimulation of the cerebellum affects only implicit processing of emotions.

On the other hand, fMRI study conducted by Scheuerecker et al. (2007) showed that the cerebellum is activated only during explicit perception of emotional facial expressions. Another line of evidence comes from studies focusing on emotional perception from an internal environment. One might expect that cerebellar patients would show impairments in gambling behaviour, as emotional processing is crucial for decision-making (Bechara et al., 2000). Surprisingly, however, normal gambling behaviour has been reported in patients with cerebellar lesions. These patients can engage in counterfactual thinking, a cognitive mechanism that allows comparison between actual outcomes and potential alternatives, and they are able to feel regret from wrong choices and adjust future decisions accordingly (Clausi et al., 2015). However, although participants were able to experience regret arising from their wrong choices and were able to anticipate their future decisions, they significantly differed in their ability to consciously report feelings of regret. Other emotions did not show differences between groups.

These findings suggest a distinction between implicit and explicit processing within the cerebellum, where cerebellar patients can implicitly adjust their choices but struggle to explicitly reflect on their emotions of regret (Clausi et al., 2015).

This duality in processing can be explained by the functional topography of the cerebellum, where different regions support different processes. While implicit and explicit

emotional processing use similar pathways in the cerebrum, explicit processing demands more cognitive resources, engaging additional neural systems (Scheuerecker et al., 2007). It is possible that a similar parallel process occurs in the cerebellum. In the next chapter, we will further explore where these different functions might be localized.

### 6.3 Medial-to-lateral gradient

Kruithof and colleagues (2022) proposed an existence of medial-to-lateral gradient, where vermal and paravermal areas are involved in basic perceptual processes whereas lateral hemispheres subservise more complex higher-order cognitive processes. The cerebellum is organized in gradients based on their functional connectivity with cerebral networks (Guell et al., 2018).

Conceptual act theory (Barrett et al., 2007; Lindquist et al., 2012; Russell & Barrett, 1999) distinguishes between two subsystems of the GEN. The “core affect” system is involved in interoception and representation of these sensations giving rise to “core affective tone” (valence and arousal). The core affect is thought to rely on the Salience network, with which both vermal lobule VI and adjacent Crus I are connected (Buckner et al., 2011; Habas et al., 2009; Sang et al., 2012). Vermal and paravermal areas of the cerebellum form anatomical connections with brain stem reticular nuclei (Dietrichs & Walberg, 1979) and the hypothalamus (Haines et al., 1997) which are both crucial parts of the core affect system. The vermis is a point of conjunction of sensory stimuli, emotional state of an individual and motor responses (Adamaszek et al., 2017). It has been shown to be a place of integration of arousal and valence (Styliadis et al., 2015), implying that the vermis might be a part of this core affect network.

However, the sensations arising from the core affect system are not meaningful unless they are attributed to a specific object. What constructs the conscious experience of emotion is the *situated conceptualization* which integrates these sensations with external stimuli and categorical information stemming from past experiences.

This system is thought to be dependent on the DMN together with the language network (Barrett, 2009). DMN is crucial for autobiographical memory, mind wandering and projecting oneself to the future (Menon, 2023). The ECN also plays an important role in managing and organizing this construction process.

Lateral portions of the left and right lobules VI and adjacent Crus I, are preferentially coupled with prefrontal cortices (Buckner et al., 2011; Krienen & Buckner, 2009). With mPFC being core region of the DMN (Alves et al., 2019; Raichle et al., 2001) and lateral PFC core region of the ECN (Menon & D'Esposito, 2022; Seeley et al., 2007), lateral cerebellum might contribute to more advanced cognitive processing of emotion via interactions with these networks.

## 6.4 Cerebellum and emotional psychopathology

As one of the starting points of non-motor research of the cerebellum was Schmahmann's CCAS, this final segment of our thesis closes the loop by exploring the cerebellum's role in clinical psychopathology. This discussion provides further evidence of its involvement in affective processing, offering deeper insights into its broader functions.

Emerging evidence suggests that impairments of cortico-cerebellar connections might be a common underlying factor of general psychopathology (Hariri, 2019). Similarly, as the G (general) factor of intelligence is predictive of other measures of intelligence, the P (psychopathology) factor is a common underlying vulnerability to experience all types of psychopathology with disorders of thought at the highest level (Caspi & Moffitt, 2018). Fascinatingly, the disruption of cortico-cerebellar tracts is the correlate of the P factor (Hariri, 2019), with a specific association with the lobule VIIb, implicated in executive functioning. As the activation of the cerebellum is consistently observed in tasks requiring monitoring of feedback in order to refine and correct one's behavioural responses (Strick et al., 2009), the impairment of the cerebro-cerebellar connections might result in deficits in the basic integration, coordination and monitoring of information underlying dysfunctional thought present in all disorders (Hariri, 2019), as demonstrated by Schmahmann's (2004) coining of the term dysmetria of thought.

We now describe several emotional psychopathologies with known cerebellar contributions to their symptomatology.

### 6.4.1 Mood disorders

Mood disorders are defined as disturbances in a person's emotional and cognitive states associated with dysfunctional regulation of these states (Adamaszek et al., 2017).

Mood disorders can be grouped into two categories:

- A) **Unipolar disorder** – characterized as a longitudinal mental state with severe depressed mood.
- B) **Bipolar disorder** – characterized as a fluctuation between manic and depressive episodes.

Molecular, structural and functional studies implicate that the dysfunction of the cerebellum as a possible biological substrate contributing to the phenotype of the mood disorders.

### 6.4.2 Unipolar disorder

Anatomical studies provide a consistent evidence of reduced cerebellar volume in mood disorders, including unipolar disorder, also known as major depressive disorder (MDD) (Frodl et al., 2008; Peng et al., 2011).

Furthermore, meta-analytic findings show decreased cerebellar responses during reward processing in patients with MDD (Zhang et al., 2013). Also functional connectivity research supports the importance of the cerebellum in unipolar disorder with the finding of altered functional cerebro-cerebellar connectivity in patients with unipolar depression consistent across studies (Guo et al., 2015; Liu et al., 2012). Furthermore, based on the differences in resting-state connectivity, it is possible to reliably distinguish patients with MDD from healthy controls (Ma et al., 2013).

The disrupted functional connectivity between large functional networks and the cerebellum particularly, cerebellar hypoconnectivity with DMN and ECN may play a crucial role in the neuropathology of MDD (Wang et al., 2023). As the DMN plays a crucial role in processing of emotions, internally directed attention and self-referential internal activity (Menon, 2023). People with MDD often misclassify positive emotional stimuli as negative.

As we have described before the cerebellum has a crucial role in the evaluation and processing of external stimuli thus the impairment of this function might be a crucial factor underlying MDD (Adamaszek et al., 2017). Moreover this claim is supported by observation

of patients with lesions in the posterior cerebellum that are unable to explicitly reflect on their emotional states (Clausi et al., 2015).

### 6.4.3 Bipolar disorder

The CCAS arising following the damage of the vermis, is expressed as changes in personality, flattening of the affect or disinhibition. People suffering from this condition have been described as flamboyant, overfamiliar or impulsive, showing regressive and inappropriate behaviour (Schmahmann & Sherman, 1998). Interestingly the CCAS share similarities with Bipolar disorder (BP) which is a psychiatric syndrome characterized by impulsive behaviour and dysregulation of emotional and attentional processes (Singh et al., 2011).

Patients with BP who suffered multiple episodes of mania have shown reduced volume of the vermis in contrast to first-episode mania patients and healthy controls (DelBello et al., 1999). This suggests a neurodegeneration of the cerebellum following multiple manic episodes. Children of parents with BP are in considerable risk of developing the disease themselves, have been shown to possess abnormalities in concentration of neurometabolites involved in the regulation of fluid balance, myelin formation and cell energy production in the cerebellar vermis (Singh et al., 2011).

Reelin is a protein involved in the positioning of the Purkinje cells during development and modulation of their synaptic functioning during adulthood. In patients suffering from schizophrenia and bipolar disorder, the expression of the reelin is markedly decreased, which results in abnormal functioning of the cerebellum (Maloku et al., 2010).

In addition to metabolic abnormalities, reduced volume of cerebellar vermis is a consistent finding in patients with BP (Baldaçara et al., 2011; Kim et al., 2013; Mills et al., 2005). Although this finding might be confounded by medication use, it still provides strong evidence for vermal involvement in the regulation of mood. Interestingly, reduced vermal volume was found also in healthy siblings of individuals with BP, suggesting that reduced cerebellar volume might constitute an anatomico-clinical marker for the risk of developing mood disorders (Schutter et al., 2012).

## 7 The present study

Although neuroimaging and clinical studies provide compelling evidence for the cerebellum's role in social cognition, these findings are largely correlational. To establish causal relationships, cerebellar research has increasingly employed neurostimulation techniques.

Neurostimulation techniques such as transcranial magnetic stimulation (TMS) can shed light on the causal relationship between a brain region and behaviour. TMS operates upon Faraday's principle of electromagnetic induction. A pulse of current flows through a coil placed on a scalp, held over the participant's head. This pulse generates a magnetic field that passes through the scalp and the skull, subsequently inducing current in the participant's brain, which directly stimulates neuronal activity. If stimulation of a specific brain area affects performance in the task, we can conclude that the brain region is necessary for the normal performance of the task (Howseman et al., 1999; Pascual-Leone et al., 2000).

TMS creates so-called "virtual lesions" where, depending on the stimulation parameters, we can transiently inhibit neuronal activity, thus creating a reversible lesion. In contrast to clinical lesions, these lesions are more precisely localized and, most importantly, temporary and reversible (Howseman et al., 1999).

Previous work of our laboratory has highlighted the utility of TMS for investigating cerebellar functions and provided causal evidence of its involvement in the processing of emotions. For instance, Ferrari et al. (2018) showed that TMS applied to the left cerebellar Crus I/II impaired both explicit and implicit emotion recognition. Our studies also provided evidence for the cerebellum's preferential processing of negative emotions. Specifically, TMS applied to the left posterior vermis significantly impaired participants' ability to distinguish between emotionally expressive body postures, with significant effects observed only for negatively valenced emotions (Ferrari et al., 2019).

More recently, we investigated the medial-to-lateral gradient proposed by Kruithof and colleagues (2022). Our findings indicated that TMS applied over the posterior cerebellar vermis have significantly impaired participants ability of basic emotion recognition, whereas TMS over the lateral posterior cerebellum affected only higher-level process, where participants needed to integrate context, which was provided to them, in order to successfully recognize ambiguous facial expressions. When, the degree of mentalizing was lower, and participants had

to recognize the emotional expressions without any context, which is however more challenging than simple recognition of basic emotions, both lateral and medial cerebellum were recruited (Ferrari et al., 2023). Thus, more demanding task recruits additional resources, similarly as in the cerebrum (Scheuerecker et al., 2007). These effects were evident only for negatively valenced emotions, showing additional support for the negative bias of the cerebellum.

Building on these findings, our most recent TMS study investigated the temporal dynamics of the medial posterior cerebellum (Ciricugno et al., 2024). While the cerebellum contributes to cortical processing by providing fine-grained temporal predictions (Ito, 2008; Leggio et al., 2011; Van Overwalle et al., 2019b), the temporal organization of these processes remains poorly understood. Classical electrophysiological methods, such as MEG and EEG, face challenges in cerebellar research due to the cerebellum's location and anatomy (Andersen et al., 2020). Moreover, they can provide only correlation evidence. Chronometric TMS, with its excellent temporal resolution (in the order of milliseconds) and ability to establish causal relationships, serves as a valuable complement to these methods, enabling a detailed examination of the timing of cerebellar processing (Sliwinska et al., 2014). Ciricugno and colleagues (2024) demonstrated that chronometric TMS applied to the left paravermal cerebellum impairs participants' ability to discriminate facial emotions when administered 100ms after the onset of stimuli, with no effects observed in earlier or later time windows. Additionally, their study revealed that the activity of the right pSTS—a crucial region of the mirror network—was causally dependent on the activation of the left paravermal cerebellum.

Considering this evidence, the present study aimed to investigate the temporal dynamics of the posterior lateral cerebellum in processing emotional facial expressions. We sought to replicate previous findings of cerebellar involvement in facial emotion recognition by examining whether TMS applied to the lateral cerebellum impairs participants' ability to recognize emotions. Additionally, we hypothesized that TMS applied to the left posterior lateral cerebellum would significantly impair emotion discrimination at a later time point compared to the medial posterior cerebellum (100ms), due to its role in more complex processing. We focused on the left cerebellum, as it has been more consistently activated during social cognitive tasks (Ferrari et al., 2022; Metoki et al., 2022; Schraa-Tam et al., 2012), likely due to its contralateral connections with the right cerebral hemisphere, which is predominantly involved in social cognition (Overwalle & Baetens, 2009).



## 8 Methods

### 8.1 Participants

Eighteen Italian university students of psychology were recruited for the purposes of the experiment (mean age = 22.10, SD = 1.63). All participants were right-handed, based on Edinburgh Handedness Inventory (Oldfield, 1971), translated into Italian. All participants had normal or corrected-to-normal vision. Before the start of the experiment participants were administered with a questionnaire translated from Rossi et al. (2011), assessing their compatibility with TMS, specifically aimed at negating possible harmful outcomes arising from administration of the TMS, such as seizures. Seizures are caused by the hyper-synchronized discharge of neuronal populations in the grey matter, however induction of seizures following TMS is rare (less than 1% in healthy population), with a slightly increased risk for patients with epilepsy (approximately 1.4% risk) (Rossi et al., 2009). None of the participants reported any history with neurological disorders, head trauma or family history of epilepsy that could produce any side effects. The study was approved by a local ethics committee and participants were treated in accordance with the Declaration of Helsinki.

### 8.2 Stimuli

The stimuli consisted of pictures of emotional facial expressions selected from the NimStim database (Tottenham et al., 2009), depicting 8 female and 8 male Caucasian faces expressing six basic emotions (happiness, sadness, surprise, fear, disgust, and anger). The faces were covering approximately 23 x 14 degrees of visual angle.

### 8.3 General procedure

Participants were sequentially presented with pairs of emotional faces belonging to two different individuals of different genders. Participants were instructed to indicate whether the two faces expressed the same emotion (two-alternative forced choice task) (Figure 7). Stimuli were displayed on a 19" screen from which participant was seated at an approximate distance of 57 cm.

Each trial began with a fixation cross appearing in the centre of the screen (2500ms), followed by the presentation of the first face (500ms), a blank screen (1000ms) and the probe

face (500ms). After the probe face, a blank screen appeared, lasting until the participants 'response. Participants were instructed to respond as quickly as possible using left and right arrow keys with their right hand (response key assignment was counterbalanced across participants). In half of the trials, faces depicted the same emotional expressions, whereas in the other half, faces depicted different emotions. In each experimental block, each primary emotion appeared the same number of times. The experimental blocks were preceded by a short training block (10 trials) without TMS. After the training trials, participants were presented with two experimental blocks, one for each TMS site.

E-prime 2.0 software (Psychology Software Tools, Pittsburgh, PA) was used to present the stimuli, deliver TMS, and acquire data. Each experimental session lasted, on average, 1 hour and 30 minutes, including instructions, administration of the questionnaire and informed consent, neuronavigation to identify the target regions, and debriefing.

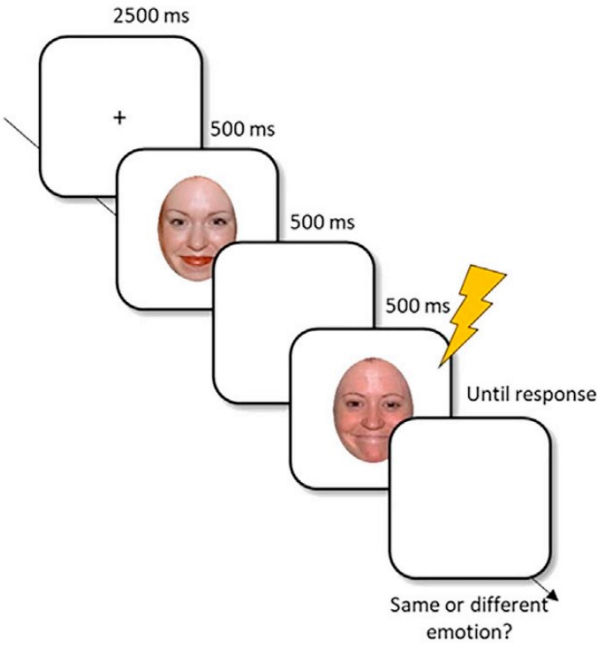


Figure 6. Scheme of the experimental task. Each trial started with a fixation cross (2,500ms), followed by the first emotional face (500ms), a blank screen (1,000ms), and the probe face (500ms). Participants were supposed to indicate, as fast as possible, whether the two faces depicted the same or different emotion, using left and right arrow keys (Ciricugno et al., 2024).

## 8.4 Resting motor threshold and motor evoked potentials

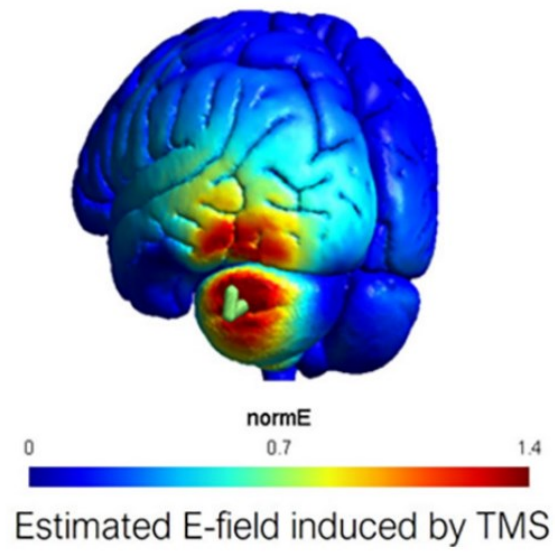
To establish the intensity of the stimulation, at the beginning of each session, a single-pulse TMS was applied over each participant's left M1, corresponding to the hand area, at increasing intensities in order to identify the individual's resting state motor threshold (RMT). Single-pulse TMS applied over M1 can elicit motor-evoked potentials (MEPs), representing the activation of contralateral muscles resulting from stimulation of the M1, which can be detected with surface electromyography (EMG). The MEPs consist of both cortical and spinal-segmental contributions and can provide quantitative measurement of cortical excitability (Bestmann & Krakauer, 2015; Rothwell, 1997) and effectiveness of the TMS stimulus in activating motor pathways (Rossini et al., 1994). RMT was defined as the lowest stimulator output at which at least 5 out of 10 consecutive TMS single-pulses evoked MEPs at least 50  $\mu$ V amplitude from contralateral first dorsal interosseous (FDI; the muscle serving index finger flexion/extension) (Rossini et al., 1994; Rothkegel et al., 2010). The MEPs were recorded from the right FDI muscles using pairs of disposable electrodes placed on belly tendon montage, with the ground electrode placed on the right wrist. In line with previous TMS studies targeting the cerebellum (Ferrari et al., 2018; Koch et al., 2007; Schutter et al., 2003), the intensity of the TMS stimulation was defined as 100% of the participants' RMT. The intensity of the stimulation was kept constant across all experimental blocks.

## 8.5 TMS over the posterior cerebellum

Online neuronavigated triple-pulse 20 Hz repetitive TMS (rTMS) was delivered over the left posterior lateral cerebellum and vertex as a control condition, using a Magstim Rapid<sup>2</sup> stimulator (Magstim Co., Ltd, Whitland, UK) connected to a 70-mm butterfly coil. Online rTMS is applied at discrete time points during the performance of a cognitive task, assessing its immediate effects, in contrast to offline rTMS which induces cumulative effects (Beynel et al., 2019). In order to modulate the cerebellar activity, creating the virtual lesion, triple-pulse rTMS was employed, with the three pulses being applied at the frequency of 20 Hz, which was found to be an effective modulator of behavioral responses in prior TMS studies targeting cerebellum (Ferrari et al., 2018, 2019; Koch et al., 2007). Participants completed two blocks of an emotion discrimination task, each corresponding to a different TMS site (left posterior cerebellum and vertex) in a counterbalanced order.

Each block included 54 trials (18 for each TMS interval). The triple-pulse 20 Hz TMS (i.e., one pulse every 50ms, for a total duration of 100ms) was administered at three different time points after the onset of the second probe face: 120ms, 220ms, and 320ms. These time windows were selected based on previous literature showing that the brain processing of emotional facial expressions occurs within 500ms. The first time window (120 – 220ms) was selected based on the results of a previous chronometric study (Circugno et al., 2024), which demonstrated that participants' performance was significantly impacted only when stimulation occurred within this interval, with no significant effects observed at earlier or later time points, suggesting that the cerebellum is not involved in processing before this time window. The left posterior lateral cerebellum was localized by stereotaxic navigation on individual estimated MRI, obtained through 3D warping procedure fitting a high-resolution MRI template with participant's scalp and craniometric points (Softaxic 2.0, EMS, Bologna, Italy). The accuracy of localization is about 5mm, comparable with precision obtained via individual MRI scans (Carducci & Brusco, 2012) and has been successfully used in our laboratory over multiple studies (Circugno et al., 2024; Ferrari et al., 2018, 2019, 2022, 2023). The anatomical Talairach coordinates (Talairach & Tournoux, 1998) of the left posterior lateral cerebellum were  $x = -31$ ,  $y = -64$ ,  $z = -27$  corresponding to the lateral lobule VI/VII, taken from a prior meta-analysis of neuroimaging studies reporting an activation in this cerebellar sector during emotional processing (E et al., 2014), with our previous TMS study (Ferrari et al., 2023) confirming causal involvement of this region in emotional processing.

The TMS coil was oriented vertically, parallel to the midsagittal line. This placement was based on previous studies indicating that this orientation of the coil is effective in modulating activity in the cerebellum (Halko et al., 2014; Jayasekeran et al., 2011; Théoret et al., 2001). Figure 8 depicts the estimated electric field induced by the Magstim Rapid<sup>2</sup> stimulator 70-mm figure-of-eight coil obtained using SimNIBS (Thielscher et al., 2015; Weise et al., 2020). During stimulation of the vertex, the handle was pointing backward. The rTMS applied close to the neck may induce involuntary muscular neck contractions. Participants were informed about these side effects and given several magnetic pulses before the start of the experiment to familiarize themselves with the sensation. During the whole experiment, participants were sitting on a chair with a chinrest meant to stabilize the head and mitigate possible contractions of the neck.



*Figure 7. Focality of the stimulation.* Induced (effective) e-field induced by triple-pulse 20 Hz TMS, adapted from Ferrari et al. (2023), who used the same ROI, TMS parameters and figure-of-eight coil as in the present experiment.

## 9 Results

Data from one participant were excluded from the analysis due to his response time (RT) exceeding 2 SD in the vertex condition. Mean recognition accuracy was 0.80, indicating that participants successfully differentiated the emotional expressions.

A repeated-measures ANOVA with TMS site (lateral cerebellum vs vertex) and TMS timing (first pulse at 120, 220, 320ms from the face onset) as within-subjects variables conducted on mean accuracy rates revealed a significant main effect of TMS site,  $F(1, 16) = 5.739$ ,  $p = .029$ , and was further qualified by the significant interaction of TMS site and TMS timing  $F(2, 32) = 3.310$ ,  $p = .049$ , suggesting that the main effect of TMS site was modulated by the of the time of application. The main effect of TMS timing was not significant ( $F(2,32) = .585$ ,  $p = .563$ ).

Post-hoc tests (Figure 9) revealed that TMS pulse applied over posterior cerebellum at 120ms significantly impaired performance relative to vertex,  $t(16) = 3.362$ ,  $p = .004$ . No differences between TMS sites were observed in the other time windows, as TMS applied at 220ms ( $t(16) = .176$ ,  $p = .86$ ) or at 320ms ( $t(16) = .525$ ,  $p = .607$ ).

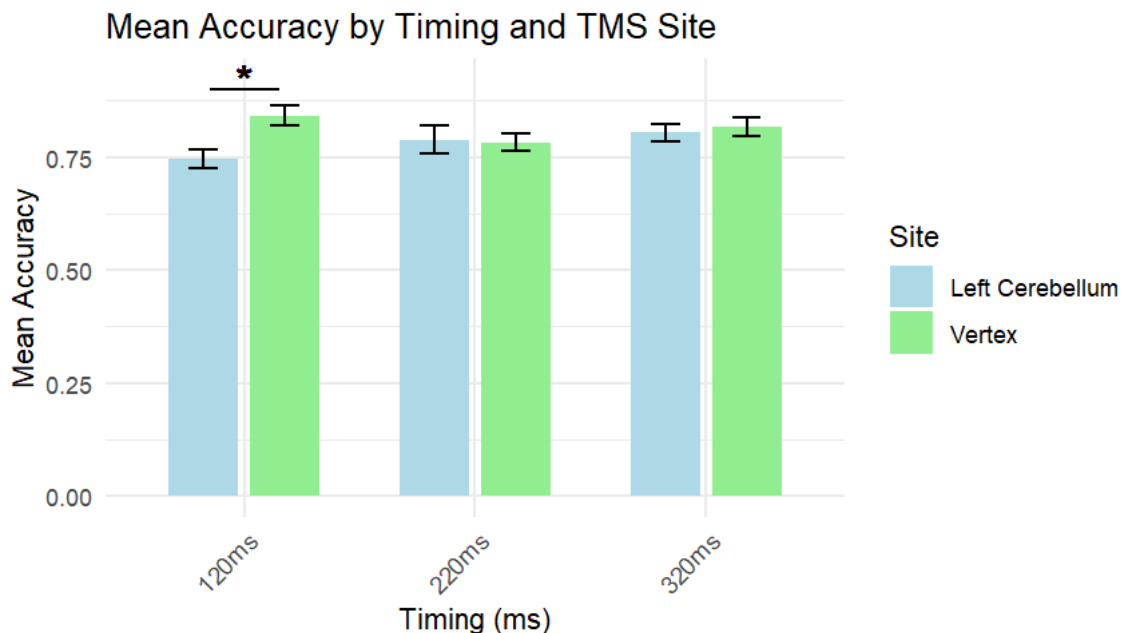


Figure 9. Mean accuracy rates (%) as a function of the TMS site (Left cerebellum and vertex) and timing of the triple-pulse 20 Hz TMS (120, 220, 320ms from the probe face onset). Error bars indicate SEM. The asterisk indicates a significant difference ( $p < 0.05$ ) between the cerebellum and vertex.

The same analysis carried out on correct RTs revealed no significant main or interactions effects (TMS site,  $F(1, 16) < 2.24$ ,  $p = .154$ ; TMS timing,  $F(2, 32) = .602$ ,  $p = .554$ ; TMS site by TMS timing,  $F(2, 132) < 1$ ,  $p = .154$ ). Mean correct RTs were 704.67ms (SD = 84.3) for posterior cerebellum TMS and 616.3ms (SD = 229.3) for cerebellar TMS.

## 10 Discussion

In this experiment, we conducted the first chronometric examination of the causal involvement of the posterior lateral cerebellum in social processing. By applying triple-pulse 20 Hz TMS to the posterior lateral cerebellum during three 100-ms intervals (starting at 120, 220, and 320ms), we found that TMS significantly impaired emotion discrimination only when administered during the 120-220ms window from the face probe onset, with no effects observed at later time windows. These results contribute to the evidence of the posterior cerebellum's causal involvement in social cognition and offer novel insights into the temporal dynamics of cerebellar processing.

The posterior lateral cerebellum has been implicated in high-level cognitive functions, with Crus I/II playing a prominent role as part of the executive cognitive cerebellum. Portions of Crus I/II have been identified as specialized regions for social cognition within the cerebellum (Ferrari et al., 2023; Heleven et al., 2019; Van Overwalle et al., 2019b; Van Overwalle et al., 2015a). These functions are mediated through interactions with the DMN and mentalizing network, to which Crus I/II are connected (Buckner et al., 2011; Van Overwalle et al., 2015a; Van Overwalle et al., 2019a).

In the emotional domain, the posterior lateral cerebellum is involved in high-order cognitive processing of emotions, engaged in cognitive evaluation of emotions and affective stimuli, integrating bottom-up and top-down processing (Adamaszek et al., 2017; Ferrari et al., 2023; Schmahmann et al., 2019).

The Crus I/II are preferentially activated during more demanding emotion recognition tasks, aiding the more primitive, mainly autonomic processing of the vermis with a cognitive processing (Ferrari et al., 2022, 2023; Van Overwalle et al., 2020b). Thus, the cerebellum seems to be organized in medial-to-lateral gradients, with lateral hemispheres subserving high-level cognitive processes.

Our current results suggest that the complex cognitive processing of cerebellar hemispheres occurs in parallel with the processing of the posterior medial cerebellum. In our laboratory's previous work, which was the first chronometric TMS study to examine the cerebellum, we demonstrated that TMS applied to the *medial* posterior cerebellum interferes with emotion recognition within the 120-220ms time window, using the same task as in the present study. No effects were observed outside this time window (Circugno et al., 2024).



Somehow surprisingly, our present results demonstrate that TMS applied to the *lateral* posterior cerebellum interferes with the performance in the same time window. This parallel processing can be explained by the cerebellar internal models, the main function of the cerebellum in both motor and cognitive processing (Adamaszek et al., 2017; Ito, 2008; Van Overwalle et al., 2020b). Internal models in the motor domain allow for fast correction and smoothing of movements, via predicting sensory consequences of planned movements (Ito, 2005; Kawato, 1999; Kawato et al., 1987). The cerebellum possesses multiple internal models in a modular fashion. Furthermore, it can combine the output signals from different models, depending on the situation and context (Imamizu & Kawato, 2009).

When we reach for a bottle, CNS has to switch between models for lifting a heavy or a light bottle, based on a cognitive cue, i.e. seeing the bottle full or empty. These functions enable us to interact with our environment in a highly flexible way.

It has been hypothesized that this role has extended during the evolution and internal models have been employed by cognitive processes in a form of sequence detection and prediction (Leggio et al., 2008, 2011; Leggio & Olivito, 2018; Molinari et al., 2008). The cerebellum encodes sequences of multi-dimensional information about external and internal events (including motor, sensory, affective, mental, and autonomic aspects) in a temporal order. As similar sequences of events occur, they trigger a predictive readout of the entire sequence before the actual events unfold in real-time. This predictive readout is then transmitted to various systems—such as motor, sensory, autonomic, attentional, memory, or affective systems—modifying their state in advance and preparing them for active involvement in the upcoming real-time events. Internal models used for social cognition may contain mental representations associated with emotional expressions, including motor schemes or contextual features which are then used by different networks embedded in the cerebellum in parallel. Indeed, it has been previously hypothesized that the cerebellum is engaged in parallel processing as the ICNs which underlie different functions of the cerebellum are represented three-fold in different cerebellar lobules (Buckner et al., 2011; Guell et al., 2018).

The posterior medial cerebellum may be a part of the core affect system, involved in interoception and the representation of these sensations, which together give rise to the "core affective tone" (comprised of valence and arousal). The core affect relies on the SN, with a prominent role of insular cortex (Lindquist et al., 2012; Lindquist & Barrett, 2012; Russell &

Barrett, 1999), with which the medial cerebellum is connected (Habas et al., 2009; Sang et al., 2012).

Additionally, the posterior medial cerebellum may contribute to emotion recognition by participating in the mirror system, as it is causally connected with the STS, a crucial region of this network (Ciricugno et al., 2024). The mirror system upon observation of actions rehearses the mental representation of the behaviour in the motor areas without any observable motor output, matching the observed action to our own behavioural repertoire (Decety & Grèzes, 1999; Jeannerod, 2001; Munzert et al., 2009), facilitating emotion recognition and empathy (Carr et al., 2003; Singer et al., 2009).

On the other hand, the posterior lateral cerebellum may be involved in the emotion construction act through its interactions with the DMN, which plays a crucial role in the interpretation of interoceptive sensations, generated by the core affect system and linking them with the external stimuli or past experiences, generating the conscious perception of emotions (Barrett, 2009; Lindquist et al., 2012; Lindquist & Barrett, 2012). Supporting this view, the Crus I has been implicated as a place of integration of valence and arousal (Styliadis et al., 2015). Additionally, Crus I is functionally connected to the ventromedial PFC (Buckner et al., 2011; Kelly & Strick, 2003; Krienen & Buckner, 2009), a crucial node of the DMN, that integrates affective and sensory cues with self-representation and autobiographical information, creating an affective meaning (Roy et al., 2012).

In summary, the temporal course of affective processing involving the cerebellum may proceed as follows: When presenting participants with images of facial emotional expressions, the core system for emotion recognition in the cerebrum (Haxby et al., 2000) categorizes perceptual information from structural properties of faces as containing emotional cues. This process occurs within approximately 100 milliseconds in humans (Adolphs, 2002). This information is subsequently channeled to the cerebellum where it matches properties with one or multiple internal models, possibly via mirroring mechanisms. When the emotional stimuli match at least some elements of the sequence encoded by these models, the whole sequence is activated which provides additional contextual information, that is used to facilitate and modulate processing in the cerebral cortex. Posterior lateral cerebellum may be using these internal models in the interaction with the DMN, within 100-200ms after onset of the stimuli. The cerebellum may possess multiple internal models of social events, which can be combined depending on the context, suggesting they may be crucial for conceptualization of emotions as

this process involves generation of predictions about causality of one's affective state based on prior experiences and context (Lindquist et al., 2012). Simultaneously, the vermis may use these internal models within the same time window, engaging in the fast identification of threatening stimuli and facilitating fight-or-flight responses by employing autonomic changes, in cooperation with the SN (Schraa-Tam et al., 2012). Thus, the cerebellum's internal models enable us not only to react swiftly and defend ourselves against potential threats but also to engage with our environment in a complex and nuanced manner.

An alternative interpretation of our results is that the TMS may have interfered with attentional mechanisms employed by the posterior lateral cerebellum. The nodes of the DMN in the Crus I are encircled by the clusters of ECN, which has an important role in the emotion construction act by managing and organizing this construction process (Lindquist et al., 2012). Whereas the cerebral cortical regions are generating signals for enhancement or inhibition of different sources of information and sensory signals, the cerebellum seems to play an important role in execution of these signals, thereby optimizing the quality of sensory information (Vandervert et al., 2024). This is particularly important for the coordination of directionality of selective attention's (Akshoomoff et al., 1997).

One potential objection to our results is the possibility that they are dependent on stimulation of the visual cortex. This concern arises from evidence showing that stimulation of the vermis can induce visual sensations, likely due to indirect activation of visual areas (Renzi et al., 2014). Indeed, TMS focality has been a matter of discussion as it has been argued, that the TMS stimulation does not spread uniformly across neighbouring cortex but rather continuously (Numssen et al., 2023). This spread is highly dependent on individual factors, specifically the individual's anatomy. The electrical field induced by TMS may not peak directly under the centre of the coil, but instead in an adjacent, more superficial region.

On the group level, constraints to interpretation may be yielded by interindividual differences in anatomy, including differences in functional topography (Numssen et al., 2023). This is particularly important to the present study as the cerebellar topographical organization of the ICNs is much more variable than the topography of the cortex (Marek et al., 2018). Nevertheless, although the spread of electric field, from our selected ROI might have also spread to the visual areas (see Figure 8), it is improbable that the effects we are reporting are dependent on indirect stimulation of the visual areas.

Ciricugno et al. (2024), in their experiment, also included the primary visual cortex (V1) as a stimulation site and an earlier time window of 20-120ms. Importantly, direct stimulation of V1 impaired performance in emotion discrimination only in this early window, with no effects in others, which confirms previous findings that the visual cortex is involved in the early processing of facial information (de Graaf et al., 2014). Also previous work of our laboratory (Ferrari et al., 2018) demonstrated that TMS effects on facial emotions perceptions upon stimulation of the cerebellum and V1 are dissociable, as TMS impairs processing when applied upon V1 or cerebellum in different time windows.

### *Limitations and future work*

Our experiment has several limitations. While we focused on the left cerebellum in this study, due to its preferential activation during social cognitive tasks (Schraa-Tam et al., 2012), other studies have also reported activation of the right cerebellum (Adamaszek et al., 2017). The role of the right cerebellum may differ, potentially influencing the time course of its contributions to affective processing, which future research could explore. Furthermore, due to the focality of the TMS we cannot precisely determine which network embedded in the Crus I/ lateral lobule VI we have specifically targeted. ROIs used in our experiment were located using an *estimated MRI*, which is a technique widely used in TMS research and has been successfully used by our laboratory previously (Ciricugno et al., 2024; Ferrari et al., 2018, 2019, 2022, 2023). Nonetheless, the real MRI images of each participant would improve the accuracy of localization and improve control for individual and group-level variation in anatomy (Numssen et al., 2023).

Moreover, as the cerebellum is more commonly activated by negative emotions (Adamaszek et al., 2017) and the temporal processing of different dimensions of affective stimuli varies (Styliadis et al., 2015), future work could employ chronometric TMS to examine the differences in temporal processing in relation to different regions of the cerebellum. Future studies could also specifically address how are the internal models employed by emotional processing. This requires the development of a new type of tasks, such as the sequencing mentalizing task (Heleven et al., 2019, Van Overwalle et al., 2019c), designed to specifically assess the cerebellar contributions to this process.

Furthermore, the exact computational mechanisms of these processes remain unclear. Despite the cerebellum's critical role in the computation of internal models, it has been largely

overlooked in computational modelling (Antonioni et al., 2024; Miall, 2003). Incorporating cerebellar internal models into computational models of emotional processing could provide deeper insights into these processes.

## CONCLUSIONS

The present study is the first to employ chronometric transcranial magnetic stimulation to examine affective processing in the posterior lateral cerebellum. Our findings confirm the established role of the cerebellum in affective processing. We also provide novel evidence for the parallel processing of affective stimuli by the cerebellum and prove that the TMS can complement classical physiological methods like EEG with causal evidence. We have demonstrated that the posterior lateral cerebellum is engaged in a simple facial emotion recognition task within 120-220ms after the stimulus onset. Similarly, the medial posterior cerebellum exhibits a comparable processing timeline, indicating parallel processing by distinct cerebellar regions.

The cerebellum's primary role, both in motor and cognitive domains, resides in the computation of internal models, enabling rapid predictions and goal-directed behaviour. These internal models facilitate processing across different cerebral networks, which form distinct connections with various cerebellar areas, providing anatomical substrates for the parallel processing of various stimuli. Impairments in this cerebellar function constitute a significant aspect of the psychopathology of numerous disorders (D'Mello & Stoodley, 2015; Hariri, 2019; Kelly et al., 2020).

Further validating our research, the cerebellum has been implicated as a crucial factor in the evolution of our species, essential for the development of human intelligence, society, and cumulative culture (Vandervert et al., 2024). Although the cerebellar role in cognitive and affective functioning remains underappreciated in neuroscience to this day, in spite of more than 20 years of ongoing research, this study contributes to the growing body of evidence, underscoring its importance in our daily life beyond motor control.

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