UNIVERSITY OF PAVIA – IUSS SCHOOL

FOR ADVANCED STUDIES PAVIA

Department of Brain and Behavioral Sciences (DBBS)

MSc in Cognitive Psychology, Neuroscience and Human Sciences

Exploring Cerebellar Contributions to Social Cognition and Mentalizing: Insights from a Transcranial Magnetic Stimulation Study

Supervisor: Prof. Chiara Ferrari

Co-Supervisor: Prof. Daniele Gatti

Thesis written by

BAHARCAN TÜRKMEN

Matriculation number: 514613

Academic year 2023/2024

For my mother and sister always next to me, for my father in heaven
and,
for the people my brain considers as “us”.

Forever yours.

INDEX

ABSTRACT

Understanding the complexities of human social cognition is essential for us to grasp the behind-the-scenes of our species. To understand mental processes, to interpret other’s intentions and beliefs, to be able to read what is behind facial expressions, or to see the not -that much- visible requires a unique ability called mentalizing. Emerging evidence suggests that the cerebellum, traditionally linked to motor functions, plays a crucial role in higher cognitive processes, including mentalizing. Our study investigated the cerebellum's role in mentalizing using transcranial magnetic stimulation (TMS) to modulate cerebellar activity while the participants engaged in the affective, cognitive, and physical Yoni task (a well-known mentalizing/theory of mind task). We stimulated the left lateral cerebellum, right lateral cerebellum, and the vertex as a control site. Our study showed that participants required significantly longer response times on cognitive tasks compared to affective and physical tasks. We also observed a potential but subtle influence of cerebellar stimulation on task performance that warrants further investigation. While our study provides valuable insights into the cerebellar roles in mentalizing, further research is necessary to expand our understanding.

Key Words: *Social cognition, mentalizing, cerebellum, cerebellar involvement, transcranial magnetic stimulation (TMS), Yoni task, higher cognitive functions*

INTRODUCTION

As Homo sapiens, we are social to the core, and our capacity for cooperation, empathy, and social bonding is deeply embedded in our biology, shaped by millennia of evolution (Sapolsky, 2017). We are equipped with an extraordinary ability to understand and navigate the complexities of the social world and for this ability, we have a mental toolkit called social cognition which is helping us to engage with others thoughts, emotions and intentions (Adolphs, 2010). Our social behaviors are a fundamental part of our daily lives since we live in a social environment and being a part of a social environment requires greater cognitive demands compared to solitary living (Dunbar & Shultz, 2007). Our social brain has evolved strategies for us to achieve levels of social interaction, collaboration, and cultural development that no other species has been able to reach, in other words, for us to *go where no other species has been (Frith & Frith, 2010).* We give social meaning to the world through our repertoire of attributions, which includes the ability to relate first- and third-person experiences, playing a key role in understanding others' emotions and intentions (Gallese et al., 2004). By using sensory data to decode nonverbal and vocal cues we infer mental states of others and anticipate their behaviors (Beer & Ochsner, 2006; Adolphs, 2010). Our ability to infer others' mental states is known as mind reading or mentalizing (Frith & Frith, 2003) which plays a vital role in social cognition. The areas involved in mentalizing are the temporoparietal junction, superior temporal sulcus, temporal poles, posterior cingulate cortex, medial frontal cortex and dorsomedial prefrontal cortex (DMPFC) (Fletcher et al., 1995; Goel et al., 1995; Amodio & Frith, 2006). Mentalizing can be divided into two key components which are the cognitive mentalizing, involving deducing beliefs and intentions, and the affective mentalizing, which relates to understanding emotions (Leslie & Frith, 1987; Shamay-Tsoory et al., 2010). The ventromedial prefrontal cortex (VM) is critical for affective mentalizing, while the dorsolateral prefrontal cortex (DLPFC) plays a central role in cognitive mentalizing (Shamay-Tsoory et al., 2006; Kalbe et al., 2010; Hynes et al., 2006). Together with anterior cingulate cortex (ACC) (Damasio, 1994; Devinsky et al., 1995; Saxe, 2006), amygdala, insula (Adolphs, 2010; Wicker et al., 2003) and inferior frontal gyrus (IFG) (Hamilton & Grafton, 2006; Van Overwalle et al., 2015) they lay the foundations of the social brain.

Recently, researchers have begun to explore the possibility that the cerebellum may play a key role in social cognition and mentalizing. Historically, cerebellar research in cognitive functions may appear to take a back seat to cerebrum studies, with most of the focus on the cerebellum’s motor functions. The cerebellum has a modest size, comprising only 10 percent of the total brain mass. Despite this small proportion, this remarkable organ is densely packed and possesses a more significant number of neurons than the entirety of the remaining brain combined (Van Essen et al., 2018). The human brain has more than 100 billion neurons (Kandel et al., 2000; Ullian et al., 2001; Doetsch, 2003; Nishiyama et al., 2005; Noctor et al., 2007; as cited in Azevedo et al., 2009) and the cerebellum contains about 80 percent of this amount, having four times more neurons than the neocortex (Azevedo et al., 2009).

The cerebellum is traditionally known for its roles in motor control (Ito, 1984) and coordination of movement (Schmahmann, 1996). It has a wide range of interconnections with the cerebral cortex (Ito, 1984) and these interconnections and the cerebellar outputs target both motor and non-motor areas. Studies conducted in the last three decades have demonstrated that the cerebellum plays a role in many cognitive functions and the map of cerebellar functioning is as intricate as the cerebral cortex functioning map (Strick, Dum, & Fiez, 2009). The introduction of non-invasive brain stimulation techniques, especially transcranial magnetic stimulation (TMS) and transcranial direct current stimulation (tDCS), has provided various new ways to study the cerebellum (Ponce, Klaus, & Schutter, 2022) and cerebellar involvement in non-motor functions has been supported by human lesion and fMRI studies (Timmann & Daum, 2007). The evidence shows the roles of the cerebellum in a wide range of cognitive tasks (Stoodley & Schmahmann, 2018) as well as affective and social processes (Schmahmann & Sherman, 1998), working memory (Desmond & Fiez, 1998), decision-making (Damasio, 1994) , theory of mind (Van Overwalle et al., 2014), social mirroring (Van Overwalle et al., 2019) and emotional processing functions (Fusar-Poli et al., 2009). Significant support for the cerebellum’s role in cognitive processes comes from the discovery of Cerebellar Cognitive Affective Syndrome (CCAS), or Schmahmann syndrome, which reveals the cerebellum's contribution to cognitive functioning through observed changes in executive function, spatial cognition, personality, and language (Schmahmann & Sherman, 1998). A meta-analysis by Van Overwalle et al. (2014) further demonstrated that cerebellar regions overlap with areas involved in sensorimotor and executive functioning, underlining the cerebellum’s consistent role in social cognition and mentalizing –one of the highest-order human functions (Van Overwalle, Ma, & Heleven, 2020). In addition to their studies, the "sequence detection theory" proposed by Leggio et al. (2011) suggests that the cerebellum detects and simulates patterns in the events around us. Therefore the involvement of the cerebellum in mentalizing is due to its role in the sequencing and predicting events. This theory suggests that the cerebellum contributes to social cognition by generating internal models of social interactions that predict outcomes based on prior experiences (Ito, 2008; Leggio & Molinari, 2015; Van Overwalle et al., 2020).

Specifically, the latest studies focusing on the posterior cerebellum (Crus I/II), due to its connections to associative cortical regions, showed its involvement in affective and social tasks (Kelly and Strick, 2003; Adamaszek et al., 2017; Sokolov et al., 2017; Ferrari et al., 2022). Interference with posterior cerebellar activity has been shown to affect the ability to discriminate emotions from facial and body expressions, highlighting its role in emotion regulation and positioning it as a key node in the social brain network (Ferrucci et al., 2012; Van Overwalle et al., 2014, 2019; Schmahmann, 2019; Ferrari et al., 2018, 2022). In addition, a consensus paper by Van Overwalle et al. (2020) emphasizes that cerebellar dysfunction is linked to various neuropsychiatric disorders, such as autism spectrum disorder (ASD), schizophrenia, bipolar disorder, and major depressive disorder.

Given these findings, there is no doubt that the cerebellum's role in mentalizing has garnered considerable attention and the discoveries are groundbreaking for the neuroscience world. Studies are increasingly exploring how cerebellar dysfunction impacts social cognition and mentalizing. Researchers are focusing on the cerebellum’s contributions to the social brain more and investigating how it supports complex processes such as empathy, theory of mind, and emotional regulation. Given these insights, it has become crucial to further explore the cerebellum's role in mentalizing, both for advancing our theoretical understanding and for practical applications in diagnosing and treating neurological and psychiatric disorders. Understanding how cerebellar impairments affect social cognition can lead to better diagnostic tools and more targeted therapies for conditions such as autism spectrum disorders, schizophrenia, and other mental health issues. Future studies focusing on the cerebellum's involvement in social and cognitive functions will be essential for unraveling the complexities of these conditions and developing more effective interventions.

1- SOCIAL COGNITION

1.1 Decoding the Social Mind: Social Cognition and Its Role in Human Interaction

Understanding oneself and others is known as social cognition, a field of interest across disciplines such as psychology, cognitive neuroscience, anthropology, and sociology (Beer, 2006). Social cognition encompasses essential cognitive processes for navigating the social world, allowing individuals to process and retain information about themselves, others, and social rules and practices (Overwalle, 2009; Beer & Ochsner, 2006). It is crucial to interact with others, which is vital for our survival and modulating our behavior in a social environment (Leggio & Olivito 2018). Social cognition enables us to exchange signals, including speech and other basic forms of communication, which are also utilized by animals (Frith & Frith, 2007). The goal of social cognition is to provide a comprehensive explanation of social phenomena (Winkielman & Schooler, in press, as cited in Frith, 2008) and perception is a critical step in decoding and encoding information about oneself and others, requiring the perceiver to understand and interpret motives and biases, which occurs at both automatic and controlled levels of processing as a part of our social cognitive functions (Overwalle, 2009). Perception involves deriving data from various sensory channels to identify nonverbal and vocal cues (Beer & Ochsner, 2006). For example, seeing a face prompts us to fill in unseen aspects, such as mental states, leading us to infer or imagine others' mental states and anticipate their behaviors (Adolphs, 2010). This process involves generating representations of possible responses to social situations (Beer, 2006). The brain's ability to establish a direct connection between first- and third-person experiences for instance, "he does and he feels” is a critical component of social cognition (Gallese et al., 2004). Social cognition includes a rich elaboration in it for instance, the way we catch the feelings of someone, what their intentions are, are they our friend or enemy is a performance that needs effort, which we do automatically. Since we are able to socially learn and interact with others, we do understand the minds of the others. For example, while simply watching a movie, we might see the main character in danger and start sweating, or watch them eat something repulsive and feel a wave of disgust ourselves. This shows how profoundly we connect with others, as we don't just observe their emotions—we actually experience and share them on a deep level. As humans, we have a rich repertoire of attributions and by using this repertoire, we give a social meaning to the world (Adolphs, 2010).

1.2 Core Concepts in Social Cognition: Theory of Mind and Mentalizing

To engage in social interaction successfully, one must acknowledge that every person has their mind, experiences, interactions, and hidden motives. Our ability to comprehend another individual's mental perspectives is known as mind reading or mentalizing (Frith & Frith, 2003) which plays a vital role in social cognition. Together with the mirror system (Rizzolatti & Craighero, 2004), they are integral for facilitating various social cognitive abilities. We typically develop this capacity to infer the mental states of others during the early years of life. We distinguish our own mental states from those of others, including their beliefs and desires; this ability is referred to as theory of mind (Amodio & Frith, 2006).

The question "Do chimpanzees possess a 'theory of mind?'" posed in a 1978 paper by Premack and Woodruff marked a significant turning point in theory of mind (ToM) research (Premack & Woodruff, 1978). Despite the complexity involved, we often infer the intentions, feelings, and social roles of others in an instinctual and automatic manner, which became a major focus of social psychology in the 1980s, spanning from animal to human studies. Our automatic interpretation of another person's thoughts or feelings based on their facial expressions is a key concept of theory of mind (Adolphs, 2010) which encompasses understanding the intentional actions of others, and the ability to quickly discern the intentions and actions of people is essential for navigating our social environment (Van Overwalle & Baetens, 2009). While theory of mind or mentalizing appears to be unique to humans and some primates, other species can predict the goals of their own species' behaviors (Emery, 2005; as cited in Van Overwalle & Baetens, 2009). These mentalizing abilities rely on the brain's default network (Beuriat et al., 2022) and they are assessed by a various of tasks, such as Sally-Anne Task (Baron-Cohen et al., 1985), Maxi and the chocolate false belief task (Wimmer & Perner, 1983) or John and Mary and the ice cream truck second order false belief task (Perner & Wimmer, 1985)

1.3 Assessing Theory of Mind: Developmental and Cognitive Perspectives

When we are interacting with a person, our brain, especially the mentalizing areas, are working hard to make us catch the cues and know something about the other person's mental states. As human beings, we have the ability to predict what the people are thinking or what they are going to do next and these kinds of questions are essential in activating our mentalizing system (Baron-Cohen et al., 1985). To test the mentalizing ability, significant tasks have been developed by various researchers.

When Premack and Woodruff (1978) argued that the primates, chimpanzees may possess a "theory of mind," they first investigated if chimpanzees could comprehend both their own and other people's mental states (Wimmer&Perner, 1983). Pylyshyn (1978) later brought another topic to the theory of mind research and proposed that having a theory of mind is having the skill "meta-representation", in other words, the knowledge of representations as relationships in addition to just representing states of affairs. To have a successful interaction and self awareness, meta representation is crucial to have as an ability. Wimmer and Perner (1983) were curious to find out from when we are able to understand deception which has a complex structure but as kids we are able to use meta-representational language, such as referring to people's 'wants' and 'beliefs,' which serves as a key indicator. Various studies have found that young children develop a substantial vocabulary and understanding of meta-representational language at different ages. For instance, Bretherton and Beeghly (in press, as cited in Wimmer & Perner, 1983) found that at the age of 2.5 years, most children spontaneously use words related to perception, major emotions, and knowledge, applying these terms equally to themselves and others. Hood and Bloom (1979, as cited in Wimmer & Perner, 1983) found that children often mentioned their own and other people's intentions when answering "why" questions by the time they are three years old. Shultz et al. (1980, as cited in Wimmer & Perner, 1983) showed that children between the ages of 3 to 5 can distinguish intentional actions from inadvertent behaviors, including errors, reflexes, and passive motions. By the time they are 4, children are able to comprehend some aspects of representation terms like "know" and "guess" (Johnson & Maratsos, 1977; Miscione et al., 1978, as cited in Wimmer & Perner, 1983) and "remember" and "forget" (Johnson & Wellman, 1980, as cited in Wimmer & Perner, 1983).

1.3.1 False Belief Understanding

According to Wimmer and Perner (1983) once we have to openly indicate the difference between one's own and another person's relation to the identical propositional content, a more complex problem arises, which is the understanding of the false beliefs. They designed an experiment to investigate this ability to understand that others can hold false beliefs. Their study had children from 3 years old to 9 years old with two stories to take into consideration. The stories had a character named Maxi as the protagonist who was looking for his chocolate and the children were asked questions according to the scenarios. In the first scenario, Maxi places his chocolate, in a specific location (location x), visible to the child participants. While Maxi is not present, the object is moved by his mother to a different location (location y), which he doesn't know. Maxi thinks the chocolate is in the original place, which is creating a critical false belief. When Maxi returns, children are being asked where Maxi will look for the object. This was the belief question which had the correct answer as “location x, the original place”. This tests whether children can understand that Maxi's statements might be influenced by his false belief and intentions. After the children gave the correct answer, the researchers asked the reality question; Where is the chocolate really? They found that children's ability to understand false beliefs develops significantly between the ages of 3 and 9. By ages 6-9, approximately 86% of children accurately understood that Maxi's actions would be based on his false belief. These findings highlight a critical developmental shift in Theory of Mind between ages 4 and 6 and the children who couldn't give the right answer failed because they lacked the ability to meta represent. With this experiment being conducted, it is important to know that the ability to understand another person’s beliefs and how this person will react on the basis of these beliefs is a cognitive ability emerging between the ages between 4 and 6 (Wimmer & Perner, 1983).

Another version of the Maxi task is called the Sally-Anne task that has been used for assessing theory of mind. In the Sally-Anne task, the logic is the same as in the puppet play paradigm of the Maxi task developed by Wimmer and Perner (1983). Baron-Cohen et al. (1985) used the Sally-Anne task in their study on children with autism to test if they develop a theory of mind. In the task, there are two babydoll protagonists, named Sally and Anne, and a hidden object, which is the marble. The experiment starts with testing the child if he/she knows the name of the doll, referred to as the “naming question.” After the child answers correctly, Sally places her marble into a basket/box and leaves. The experimenter then moves the marble to Anne’s hidden basket/box while Sally is away. Upon Sally’s return, the experimenter asks the belief question, which is essential to the study. The experimenter asks, “Where will Sally look for her marble?”. The children have to point to the previous place, considering that Sally didn't see the location change, if not, they fail the belief question. The control questions are "Where is the marble really?" for checking reality and "Where was the marble in the beginning?" for checking memory. In this study by Baron-Cohen et al. (1985), they found that the results were different for the normal and autistic children. Only 4 out of

20 children with autism passed, highlighting a specific theory of mind deficit in autistic children, despite their higher mental age or general intelligence.

Flavell, Flavell and Green (1983) conducted a study investigating if the children aged 3 to 5 years could distinguish and identify real versus apparent object properties (color, size, and shape), using a few plastic objects from a joke shop. A fake rock which is actually a sponge and a pencil which is actually a rubber, a puppet hand toy of Charlie Brown that, when covered with a white handkerchief with eyes and mouth of felt, looked like a ghost; a white index card that looked pink when placed behind a piece of pink plastic. The first question for the task was “When you look at this with your eyes right now, what does it look like (what color does it look like)?” After the child answered, the experimenter agreed with his/her answer. For the reality check part, the experimenter squeezed the imitation rock and gave it to the kid to squeeze and asked “What is this really, really? Is it really, really a (rock) or really, really (a piece of sponge)?” and “When you look at this with your eyes right now,does it look like a (rock) or does it look like (a piece of sponge)?”. They found that while 3-year-olds can distinguish reality from appearance, older children sometimes make errors, likely due to metacognitive limitations.

Wimmer and Perner (1983) also used a Smarties tube to investigate children's understanding of false beliefs. The Smarties task included a Smarties tube, which had pencils inside and the children were asked to say what was inside the tube. The children said Smarties, which was expected. After the children’s answers, the experimenter showed what was really inside the Smarties tube, the pencils. Following this reveal, the children were asked, "What did you think was inside the tube before it was opened?" This question tested the child's memory and understanding of their initial false belief. The second question was, "What would another person, who hasn't seen inside the tube, think is inside?" Here, the question assessed the child's understanding of another person's false belief. The researchers revealed that in the Smarties task, a large part of the children who were 3 years old had difficulties identifying their initial false belief and predicting another person's false belief. This ability to comprehend and distinguish between beliefs and reality, which is crucial for social cognition, typically develops more fully by age 4 (Perner et al., 1987).

1.3.2 Second Order False Belief Understanding

The tasks mentioned up until now represent the tasks for the first order false belief (first order reasoning). Compared to the second order false belief or second order reasoning tasks, the first order reasoning tasks have less complex language. A second-order false belief is an understanding of what one person believes about another person's belief, which may be incorrect from an observer's point of view. According to Perner and Wimmer (1985), first-order false beliefs can explain the physical interactions between individuals and objects, but they are ineffective at capturing social interactions. The only way to comprehend human interaction is to examine how minds interact, which needs considering what other people believe about other people's thoughts (second order beliefs), and beyond that, what people believe that other people believe about themselves (higher order beliefs).

Perner and Wimmer (1985) published a paper named "John thinks that Mary thinks that…" which summarizes the essence of the second order false belief tasks. They assessed the ability of the children in understanding second order reasoning, in other words, second order false belief. Their research design had two characters, John and Mary who wanted to buy ice cream from an ice cream truck. The ice cream truck is supposed to be in the park but there is a sudden location change and only John is getting informed about this location change. Mary doesn't know the ice cream truck is being moved to the church at first but later she accidentally learns about the fact that it is going to be moved. Still, John is unaware that Mary learnt the change of location. The main question of this ice cream task is, "Where does John think Mary has gone?" which to answer, the children need to understand that John has a false belief about Mary's beliefs. The second main question is "Does John know the ice-cream man talked to Mary?" and to answer this question, the children need to have the ability to understand second order false belief. In their study, Perner and Wimmer found that the older children, ages above 8, were better at finding out what one character thought another character believed. For the story of the second experiment, they added a garage where the van went because its tire broke. The key aspect of this story is that it introduces a false belief for both characters regarding the van's location. The experiment tested whether children could understand that John still thinks Mary believes the van is at the church, even though it never arrived there. Contrary to the expectations of the researchers, the results showed that children did not perform better when both characters had a false belief. In fact, performance tended to be slightly better in the original condition (where the van was present at the church) compared to the new condition (where the van was towed to a garage and was no longer at the expected location).

In a paper by Hollebrandse, van Hout and Hendriks (2011), the first and the second order reasoning was tested on children and their performances were investigated in the context of the language as well. The researchers were interested in if language is affecting the reasoning ability. In their study, they used both verbal and nonverbal tasks to assess the performances. The stories they use include the manipulation of the beliefs of two protagonists to assess children's understanding. For the first-order beliefs tasks, both protagonists start with the same belief, and then one protagonist's belief changes without the other knowing. Their verbal false belief tasks were based on the ice cream truck story by Wimmer and Perner (1985). In their experiment, there were two characters, Sam and Maria, who thought there would be chocolate chip cookies at the church bake sale. Later in the story, Sam’s mother tells him that there will be pumpkin pie, but Maria doesn't get this information. Then Maria discovers that only brownies are left, while Sam remains in the dark. Sam now thinks they are selling pumpkin pie (a first-order belief), whereas Maria knows the truth (brownies) but believes that Sam still thinks they are selling cookies (a second-order belief). For the non verbal false belief tasks, the attention was drawn only to the contents of the boxes and the participants had to observe the contents of the boxes. The mental state words such as think or believe were excluded and the experimenters tried not to use the mental states words. For the tasks, the participants had to watch short movies. The task was presented as a game in two parts. In the first part, participants tracked what the observer in the movie knew about the box's contents or the object's location (first-order trials). In the second part, participants were told the game continued but with a new player: an additional observer in the movie. Participants then tracked what this new observer knew about the box's contents and the other observer's beliefs (second-order reasoning). The events in the second-order movies were similar to the first-order ones but introduced a second-order false belief. For example, the man incorrectly believed the woman thought there was an apple in the box, while she believed there was a basket; in reality, there was a turtle. Bart Hollebrandse, Angeliek van Hout and Petra Hendriks (2011) found that the second order false beliefs consist of more complex understanding the children are having difficulties comprehending the second order false beliefs as they performed better on the first belief reasoning tasks. The children performed better with the verbal tasks which included language. This shows that the language plays a crucial role in helping children navigate these complex mental states and their results were in line with Perner and Wimmer’s (1985) results.

Another significant task that was used in theory of mind research was the triangle animation task. In 1944, Heider and Simmel used the triangle task aiming to create new stimuli that would specifically elicit mental state attribution through their motion characteristics. They showed moving geometric shapes such as triangles, rectangles and circles to the participants and they wanted them to interpret the movements. The movements were classified as goal-directed, theory of mind, and random. The goal-directed animations demonstrated interactions without attribution to mental state, the Random animations showed aimless movement, and the ToM animations showed interactions that required mental state knowledge. The triangles differed in size, there was a small and a large triangle. The circle was moving within a rectangular house. The participants attributed human-like motives and emotions to the shapes by describing the movements as intentional actions. Their study showed that people can attribute human-like intentions and complex social narratives to abstract stimuli. For example, when the big triangle was behind the small triangle and they moved, participants interpreted the movements as chasing, fighting, or hiding which are the human-like interactions. The participants assigned emotions to the geometric shapes in addition to the movements' intended purposes. The triangle test also examines how people perceive and interpret social conduct in the absence of clear social information because there were no verbal cues (Heider&Simmel, 1944). Springer et al (1996) used Heider and Simmel's task on younger children around the age of 3, 4 and 5 and concluded that sensitivity to these patterns of motion emerges gradually, with significant improvements evident by age 5, indicating a developmental progression in understanding interpersonal events through motion. Even though the studies mentioned that the age for attributing the mental states to the animated shapes are around 5 years, Montgomery and Montgomery (1999) explored how would preschoolers perform in the tasks and made children watch a circle move persistently towards a target. The children, who were 3 years old, correctly inferred the circle's goal, even if they struggled in the non-goal conditions. When the non-goal condition was adjusted, performance improved across all ages. The findings show that by age 3, children can detect intentions from movement patterns and differentiate these from the actual outcomes. In 2000, Abell, Happe and Frith investigated how different groups, such as children with autism, attribute mental states to animated shapes by using Heider and Simmel's (1944) moving animations task. They looked for the performance of the children, both autistic and normal developed children and compared their understanding of mental states. They tested the theory of mind and understanding false beliefs ability with the famous and efficient theory of mind tasks such as The Sally-Ann test (Baron-Cohen et al., 1985) and Smarties test (Perner et al., 1989) and the Ice-Cream story (Perner & Wimmer, 1985). In their investigations, they found that the children with autism struggle with mental states attribution in a dynamic and non verbal context even though they passed the false belief tasks before. Their findings show that mentalizing has a complex structure and it is important to have interventions tailored for supporting individuals on a deeper level.

1.3.3 Faux Pas Understanding

In addition to the other theory of mind abilities, one crucial skill to have is the ability to comprehend and recognize faux pas. Faux pas stands as a social blunder, a social mistake and it happens when someone says something they shouldn't have said, unaware that they shouldn't say it (Stone, Baron-Cohen, & Knight, 1998). In other words, a faux pas occurs when a person makes a socially inappropriate or tactless comment without being aware of the relevant contextual information. Faux pas has two aspects. The first is the cognitive aspect where to comprehend faux pas, the listener must understand that the speaker is saying something inappropriate, something that he or she should not have said and the second one is the empathic aspect in which the listener is aware that hearing the inappropriate things that have been said would hurt or upset the character (Stone, Baron-Cohen, & Knight,1998). In the faux pas tasks, the researchers had different stories which involved social situations and characters. They wanted to test if the children could interpret these advanced theory of mind situations. After each story, the children were asked a series of questions to determine if they recognized that a faux pas had occurred, could identify what the faux pas was, and understood the impact it might have on the listener. One of the stories they had was about a woman named Mary. Mary says, "I don't think I've met this little boy," to a child's mother. In reality, the child is a little girl. The speaker made the comment out of a mistaken belief, not realizing that it might be upsetting for the parents to have their daughter mistaken for a boy.

After the story has been told to the child, they asked four questions. They had a faux pas detection question which was; In the story did someone say something that they should not have said? This was to understand if the child is able to realize that there is faux pas happening. AFter detection, they had the identification question which was; why did they say that they should not have said? Then they asked the comprehension question which is different for every story and this question is making sure that the child understood the story that had been told such as "Why shouldn't Mary have said that?". And the final question was a false belief question; did they know/remember that? (Stone, Baron-Cohen, & Knight,1998). Baron-Cohen, Jolliffe, Mortimore, and Robertson (1997) found that children between the ages of 9 and 11 typically begin to understand faux pas. They also discovered that there was a gender difference where by the age of nine, girls could score highly on our novel faux pas detection test, whereas boys could do so by the age of eleven. The faux pas test requires a more complex understanding of the theory of mind, which can be understood by the same study where the children aged around 7 or 8 did pass second order belief tasks while they failed the faux pas tasks.

1.3.4 The Yoni Task

In 2007, Shamay-Tsoory and Aharon-Peretz introduced the Yoni theory of mind task. Their aim was to distinguish the affective and cognitive aspects of theory of mind and exhibit the different underlying brain areas for different types of theory of mind. They saw the need of a comprehensive tool to access both the cognitive and the affective aspects of theory of mind since the traditional theory of mind tasks usually focus only on the cognitive aspects of theory of mind, for instance, the false belief understanding. For the second-order false belief tasks, participants need to have the ability to distinguish between the speaker's knowledge and the listener's knowledge, which is referred to as cognitive theory of mind. On the other hand, tasks involving faux pas require an empathic appreciation in addition to the ability to distinguish the knowledge of both parties, which is referred to as affective theory of mind.

The affective theory of mind includes understanding the emotions and intentions of another person. They designed a series of computerized trials that wanted participants to make conclusions from both verbal and nonverbal cues. In the tasks, there is a character called Yoni and the participants must infer his thoughts and emotions. The participants infer based on his eye gaze, facial expressions and the contextual clues provided by the surrounding images of the task. Participants are asked to identify Yoni’s thoughts and feelings based on the visuals that are categorized as fruits, animals, and objects. Through this setup, the task assesses the cognitive and affective theory of mind with a detailed evaluation of mental state attributions (Shamay-Tsoory and Aharon-Peretz, 2007).

It has been proposed that the theory of mind skills could have lateralized nature (Baron-Cohen et al., 1994; Shamay- Tsoory et al., 2005; Shamay-Tsoory an Aharon-Peretz, 2007) and it is crucial to investigate the patients with unilateral lesions. In their study, Shamay-Tsoory an Aharon-Peretz, 2007 have especially mainly focused on the ventromedial frontal lobe's roles in theory of mind based on the idea of the researchers that this area would be especially engaged in affective theory of mind and the impairments in this area would affect the affective aspect of theory of mind, rather than the overall theory of mind. In order to investigate different brain areas for different types of theory of mind aspects, they developed two theory of mind tasks. They investigated 49 participants with localized brain impairments and 44 healthy control subjects. They conducted the tests at least six months post-trauma or surgery, ensuring patients were in the chronic phase of recovery. They had 3 conditions which were cognitive, affective and physical, physical being the control one. For the cognitive conditions, the facial expressions and the verbal cues of Yoni character was emotionally neutral, for instance for the first cognitive condition; "Yoni is thinking of…" For the affective conditions, the facial expressions and verbal cues provided affective information, for instance for the first order affective condition; "Yoni loves…Yoni doesnt love…". They used both positive and negative statements for both cognitive and affective conditions however they didn't find a significant result on the valence effect on reaction time or accuracy rate. For their second order conditions, for cognitive, affective and physical conditions, they used four stimuli which included face images and the choice of the correct response requires understanding of the interaction between each of these figures and Yoni's mental state. Thus, while the second order cognitive requires understanding beliefs about others' beliefs and desires, for instance, Yoni is thinking of the toy that wants, the second order affective involves understanding of one's emotions in regard to the others' emotions, such as Yoni loves the toy that ... .loves. Their study was one of the first ever to suggest that the patients with different lesion locations had different difficulties in the two types of theory of mind. They indicated that ventromedial affecting the affective theory of mind tasks and lesions in this area resulted in difficulties understanding of emotions and irony. The damage in the prefrontal area, dorsolateral and ventromedial together, affected the cognitive theory of mind performance. They showed that there is some overlap between cognitive and affective mentalizing abilities, however they are also independent with different neuroanatomical bases.

1.4 Neural Correlates Of Social Cognition

Human beings are inherently social creatures, and social behaviors are fundamental to our species. While social activities are universal across species, Homo sapiens, in particular, experience and engage in social interactions throughout their daily lives (Adolphs, 2010). Living within a social environment and being part of a social group impose greater cognitive demands compared to solitary living (Dunbar & Shultz, 2007). The brain, the most metabolically costly organ, has evolved strategies for group living that benefit both individuals and the collective (Silston et al., 2018).

The neural foundations of social cognition are rooted in a complex network of brain regions that allow us to understand and respond to the thoughts, emotions, and intentions of others. The brain's functions, including those related to hearing, vision, language, and memory, are recruited in social cognition, even if not exclusively (Beer, 2006). The visual, auditory, and visceral systems, along with neural systems involved in semantic or declarative knowledge, facilitate the perception and encoding of social information (Beer, 2006). Key brain regions associated with social cognition include the frontal lobes (especially the orbitofrontal and medial prefrontal cortices, and the cingulate cortex), the temporal lobes (including cortical and subcortical regions such as the amygdala), the fusiform gyrus, and the somatosensory cortices (Adolphs et al., 2001; Beer et al., 2004; Beer, 2006).

Brothers (1990) introduced the concept of the "social brain," suggesting that a specific group of brain regions is dedicated to social cognition. Brothers, Ring, & Kling (1990) discovered that neurons in the amygdala of awake, behaving monkeys exhibited responses to specific, complex social stimuli, such as the approach of another monkey. They argued that the components of this system include the amygdala, orbital frontal cortex, and temporal cortex. In addition, Amodio and Frith (2006) highlights the role of the medial prefrontal cortex and the adjacent paracingulate cortex in social cognition. Brothers proposed that social pressures drove the brain to develop cognitive and affective processes, leading to the evolution of the social brain, which underpins appropriate social conduct, emotional reactivity, and social cognition (Burns, 2006).

The social brain network comprises a variety of brain regions. Damasio (1994) highlighted the critical roles of the prefrontal cortex in decision-making, emotion regulation, and social behavior with his widely known case of Phineas Gage, while he was also emphasizing the roles of the prefrontal and anterior cingulate cortices in social cognition. The medial prefrontal cortex (MPFC) is constantly active while we are activated when thinking about one's own and other people's mental states (Saxe, 2006). Anterior cingulate cortex (ACC), has a significant role in social interactions, such as bonding and social behavior regulating (Devinsky et al., 1995). Particularly the gyrus region (ACCg), plays an essential role in social cognition and it is especially important for processing and responding to social information related to comprehending other people's motivations and behaviors (Apps, Rushworth, & Chang, 2016). Damage to the ACC exhibits social behavioral changes (Devinsky et al., 1995). Also the ACC have been found to be linked by the social cognitive impairments (Jenkins et al. 2014). In addition, temporo-parietal junction (TPJ) activity is related to spatial and mental perspective-taking which is related to false belief understanding understanding false beliefs, meaning that its involved in representing mental states (Blanke et al., 2005; Aichhorn et al., 2005; Apperly et al., 2004; Saxe & Kanwisher, 2003; as cited in Frith & Frith, 2007).

Research indicates that both the posterior superior temporal sulcus (pSTS) (Amodio & Frith, 2006) and the superior temporal sulcus (STS) (Pelphrey, Morris, & McCarthy, 2004) are crucial in social cognition, particularly for understanding others' intentions through their actions. Specifically, the right pSTS is involved in processing and representing observed intentional behaviors (Saxe et al., 2004). Amygdala is in charge of attaching value to objects such as faces and how we interpret and respond to social cues (Winston et al., 2002; Frith & Frith, 2007). It is involved in social cognition by evaluating the emotional significance of social stimuli, particularly in processing facial expressions and making judgments about trustworthiness, playing a key role in recognizing and interpreting emotions, which is essential for understanding and navigating social interactions (Adolphs, 2010). The insula, particularly the anterior insula, plays a key role in social cognition by facilitating the emotional and affective understanding of others' experiences, especially in the context of empathy (Singer, 2004). Its activation when observing disgusted facial expressions and experiencing disgust from odors highlights its role in recognizing and mirroring emotions in others, suggesting a shared neural foundation for both experiencing and identifying emotions like disgust, which is crucial for social interactions (Wicker et al., 2003). In addition, action execution and action observation leads to activity in the inferior frontal gyrus (IFG) and interparietal sulcus (IPS), highlighting their crucial roles in motor cognition and social interaction (Hamilton & Grafton, 2006; Rizzolatti & Craighero, 2004; as mentioned in Frith & Frith, 2007). Additionally, the social brain network includes extensive areas across all lobes and parts of the cerebellum (Van Overwalle, D'aes, & Mariën, 2015).

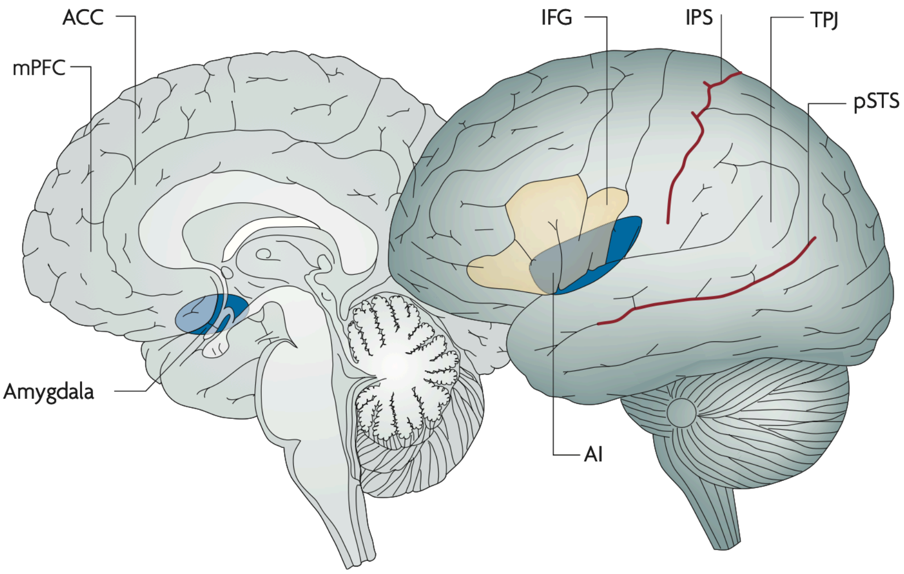


Figure 1; The Social Brain Regions (Blakemore, 2008)

1.4.1 The Mirror System

Our ability to understand and empathize with others is rooted in the activation of the same neural structures that are involved when we perform actions or experience emotions ourselves and this activation is the essence of social cognition (Gallese et al., 2004). Rizzolatti and Craighero (2004) introduced the concept of the "mirror system," a network of brain areas activated both when performing an action and when observing someone else performing the same action. They discovered that neurons in area F5 fire during both action execution and observation, leading to the identification of these as mirror neurons (Di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996). This mechanism is an essential part of social cognition and might support certain aspects of social learning, without the need for higher-level conceptual reasoning (Gallese et al., 2004). In humans, mirror systems extend beyond action to include emotional processing (Singer et al., 2004; Botvinick et al., 2005; as cited in Frith, 2008) and touch (Blakemore et al., 2005). Our ability to predict others' actions also relies on the social brain (Frith, 2007). Molenberghs et al. (2012) gathered data from 125 human fMRI investigations to determine which brain regions are active during tasks intended to activate the mirror mechanism. They demonstrated that the areas in the brain that are involved in the activation or social stimuli, in other words, the mirror system were widespread in the brain with constant activation. Their data show that the inferior frontal gyrus, ventral premotor cortex, and the inferior parietal lobule were activated with the addition of early visual cortex, the parts of the limbic system and the cerebellum. This finding shows that, mirror system includes auditory, somatosensory, and affective processing areas, in addition to the motor related areas, highlighting the versatility and broader functional significance of the mirror neuron system in humans.

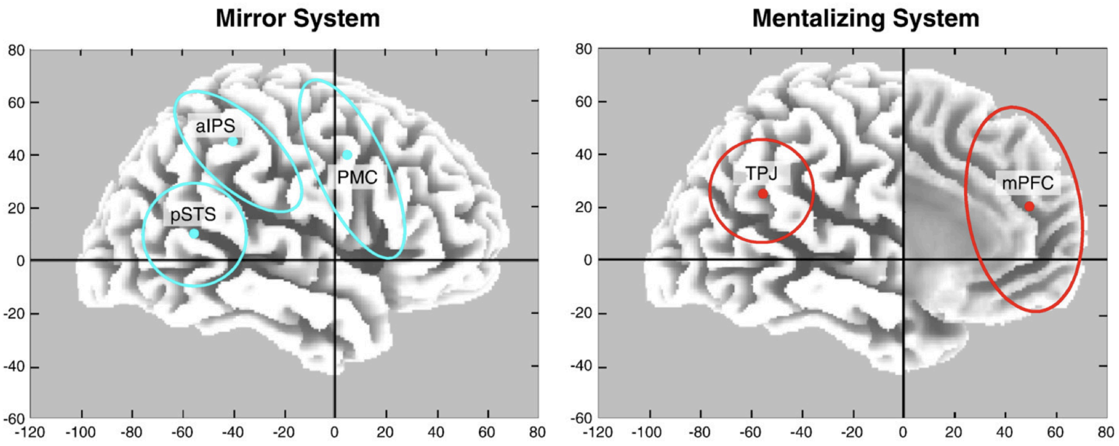


Figure 2; Mirror and mentalizing systems on the Talairach atlas (Van Overwalle & Baetens, 2009).

1.5 Cognitive and Affective Mentalizing Networks

Our capacity to explain and predict the behavior of others in terms of their mental states (beliefs and desires)—referred to as theory of mind or mentalizing (Leslie & Frith, 1987)—consists of two components. The cognitive aspect, where we deduce others' beliefs and intentions, is called cognitive mentalizing, while the affective aspect, where we perceive others' emotions and feelings, is termed affective mentalizing (Shamay-Tsoory, Harari, Aharon-Peretz, & Levkovitz, 2010; Arioli, Cattaneo, Ricciardi, & Canessa, 2021). While the areas involved in the mentalizing network are the temporoparietal junction, superior temporal sulcus, temporal poles, posterior cingulate cortex, medial frontal cortex and dorsomedial prefrontal cortex (DMPFC) (Fletcher et al., 1995; Goel et al., 1995; Amodio & Frith, 2006), recent studies have been found that the different types of mentalizing has different neural pathways. The research has been focused on these different aspects of theory of mind and the distinct parts of affective and cognitive theory of mind (Baron-Cohen & Wheelwright, 2004; Kalbe et al., 2007; Kalbe, Schlegel et al., 2010). For instance, false belief tasks are used to assess cognitive mentalizing by requiring comprehension of the difference between the knowledge of the listener and speaker, while faux pas and irony tasks relate to affective mentalizing (Shamay-Tsoory et al., 2006). Shamay-Tsoory et al. (2005) suggested that affective mentalizing is akin to empathy. Further evidence for the distinction between cognitive and affective mentalizing comes from studies showing that these two aspects involve different underlying networks (Corradi-Dell'Acqua et al., 2020; Leopold et al., 2012; Shamay-Tsoory, Tibi-Elhanany, & Aharon-Peretz, 2006; Shamay-Tsoory & Aharon-Peretz, 2007). For instance, patients with lesions in the ventromedial prefrontal cortex (VM) in a study by Shamay-Tsoory et al. (2006) exhibited impaired affective theory of mind understanding but performed normally on cognitive theory of mind tasks, suggesting that the VM cortex is crucial for processing the emotional aspects of social cognition, while cognitive aspects remain unaffected by VM damage (Shamay-Tsoory, Tibi-Elhanany, & Aharon-Peretz, 2006). Neurostimulation studies have explored these neural networks (Kalbe et al., 2010; Krause, Enticott, Zangen, & Fitzgerald, 2012), and clinical studies have further detailed different underlying neural pathways (e.g., Shamay-Tsoory & Aharon-Peretz, 2007; Shamay-Tsoory et al., 2007; Ruitenberg, Santens, & Notebaert, 2020). A functional magnetic resonance imaging (fMRI) study by Hynes et al. (2006) provided significant evidence for the distinction between cognitive and affective mentalizing. Their research demonstrated that the medial orbitofrontal lobe is engaged in emotional, as compared to cognitive, perspective-taking. The medial and orbital PFC are involved in affective perspective-taking, while dorsolateral prefrontal areas are involved in the cognitive aspect (Hynes, Baird, & Grafton, 2006). The study by Kalbe et al. (2010) presents empirical support for the functional separation of affective and cognitive theories of mind (ToM) by highlighting the role of the dorsolateral prefrontal cortex (DLPFC) in neural networks mediating cognitive ToM (Kalbe, E., & Schlegel, M., 2010).

Further technological development of modern neuroscientific methods, including functional magnetic resonance imaging (fMRI), have advanced our understanding of how people judge the actions of others, including their intentions, ambitions, desires, beliefs, and characteristics (Van Overwalle & Baetens, 2009). Early research into the neural basis of mentalizing identified a distinctive network of brain activations when participants read stories about social interactions. This network includes the temporoparietal junction, superior temporal sulcus, temporal poles, posterior cingulate cortex, and medial frontal cortex (Fletcher et al., 1995; Goel et al., 1995; Amodio & Frith, 2006). In addition to these areas, recently cerebellum, especially the posterior cerebellum, also gained attention with its involvement in the mentalizing network (Van Overwalle et al., 2014).

2- IMPAIRMENT OF SOCIAL COGNITION

2.1 Social Cognitive Impairments: The Impact of Social Cognition Deficits Across Psychiatric and Neurodevelopmental Disorders

Human beings may be similar to animals in many ways, for instance, both species use cues like facial expressions, body posture, and tone of voice to predict others' behavior and communicate (Frith & Frith, 2007). However, our difference is, we do not just respond, we go beyond just reacting to a behavior. We are also able to comprehend and react to the mental states of others, including their intentions, knowledge, beliefs, and desires (Stone, Baron-Cohen, & Knight, 1998). Thus, social cognition is an essential component of human functioning (Leggio, 2018).

Social cognition encompasses a wide range of aspects in various forms and theory of mind is one of the most critical dimensions (Overwalle, 2009; Beer & Ochsner, 2006). There is a considerable amount of disorders linked to social cognition and affecting individuals lives (Beer, 2006). The impairments usually involve critical decline in the comprehension and management of social interactions. The quality of life is being affected by these impairments. Theory of mind plays a crucial role in social cognition (Frith & Frith, 2003) and mentalizing has been found to be impaired in a variety of disorders. Impairments in theory of mind can remarkably influence the social cognitive abilities since social cognition is more related with the community functioning rather than it is related to the neurocognition (Fett et al. 2011).

2.2 Disorder-Specific Impacts of Social Cognition Deficits

In a study of Cusi et al. (2012) they showed that the patients who had mood disorders exhibited increased activity in emotion related brain regions and reduced activity in frontal regions responsible for emotion regulation and higher cognitive functions. Theory of mind and emotion recognition are the aspects of social cognition and in their study they showed that individuals who had mood disorders had impaired theory of mind abilities. They included patients with major depressive disorder (MDD) and bipolar disorder and showed that the impairments are associated with altered or reduced neural activity in brain regions responsible for both cognitive and affective processes. These findings show that during social cognitive processing in people with mood disorders, higher-order cognitive structures generally do not suppress limbic and emotion-related structures therefore they are associated with poor clinical and functional outcomes. Gregory et al. (2002) found that impairments in mentalizing, especially in theory of mind, have significant effects on patients with disorders such as frontal variant frontotemporal dementia (fvFTD). Patients with fvFTD frequently have difficulty identifying social faux pas, reading the emotions of others and predicting others' behavior based on mental states. This leads to inappropriate behavior in society and lack of empathy, which results in difficulties in maintaining personal relationships. Patients with Alzheimer's disease are affected less severely than the frontotemporal dementia (fvFTD) patients, however they still experience significant impacts on cognitive functioning. They are having difficulties on more complex tasks that require higher cognitive load while having the basic theory of mind skills. They may struggle with second-order false belief tasks, which demand the ability to consider what one person thinks about another's thoughts which may result in misunderstandings in social interactions and withdrawal and reduced engagement with others.

2.2.1 Impact of Social Cognition Deficits in Autism Spectrum Disorder

Autism spectrum disorder is widely recognized for its profound impact on social cognition as well. Autism refers to a variety of neurodevelopmental disorders mainly characterized by prominent challenges in social interaction. People who have autism spectrum disorder exhibit distinctive social behaviors such as avoiding eye contact, having trouble controlling their emotions, and having trouble understanding or reacting to the emotions of others (American Psychiatric Association, 1980). It is a well-known condition where deficits in social cognition are prominent. A pioneering paper by Baron Cohen&Leslie&Frith (1985) proposed that theory of mind (ToM) is strongly related to autism and is essential to comprehending the social impairments that are frequently seen in individuals with the condition. In their study, they have used puppet play paradigm Sally Anne task (Wimmer & Perner, 1983). Their control groups were the typically developed preschool children and the children who had down syndrome. In their Sally-Anne experiment, The critical question was whether the children could understand that Sally would have a false belief about the marble's location and would therefore look in the original place where she left it, not where it had been moved. While the typically developed and down's syndrome children correctly identified the original location, most of the children who had autism pointed to the new location where the marble actually was, failing the Sally-Anne task despite that their ages were higher than the control groups. These results indicated that autistic individuals lack a fully developed theory of mind (Baron-Cohen, Leslie, & Frith, 1985).

2.2.2 Impact of Social Cognition Deficits in Schizophrenia

Bleuler was the first person ever to use autism to refer to a characteristic of schizophrenia called "autistic aloneness". This term referred to a withdrawal into the self. In 1991, Frith et al. proposed that the 'qualitative impairment in social interaction, a key diagnostic criterion for autism which was identified by DSM-IV, may be explained by a deficit in Theory of Mind. They also suggested that autism and schizophrenia might be caused by a similar cognitive deficiency (Frith & Frith, 1991). While the autism symptoms are visible starting from infancy, individuals with schizophrenia often do not exhibit abnormal social interactions till their adulthood (Frith, 2004). In 2004, Lee et al., aimed to determine whether or not individuals with schizophrenia exhibit disruptions in the brain systems underpinning social cognition, especially the theory of mind. Their review focused on mentalizing and empathy in the individuals with schizophrenia. They combined findings from a wide range of studies to understand how particular neural networks, especially in the frontal, temporal, and limbic areas, are engaged in social cognition and how dysfunctions in these networks might lead to the social and cognitive impairments observed in schizophrenia. The review shows that theory of mind is frequently impaired in people with schizophrenia which leads to thought disorders and delusions as in challenges in distinguishing between real and imagined experiences. These characteristics result in difficulties in interpreting social signals, understanding others' beliefs and intentions.

2.2.3 Impact of Social Cognition Deficits in Bipolar Disorder

In 2003, Kerr, Dunbar, and Bentall investigated if the patients with bipolar disorder would have theory of mind deficits similar to the patients who had schizophrenia. They examined a total of 63 patients with manic and depressive episodes, patients in remission and control individuals. They used a Theory of Mind (ToM) task that was previously employed in research on schizophrenia by Frith and Corcoran (1996). The patients in the manic and depressive episodes found to have decreased performance on theory of mind tasks. Both manic and depressed patients who showed poor performance usually struggled with tasks that required understanding others' false beliefs, which demonstrated that cognitive deficiencies are frequently associated with the active phases of the condition. In 2005, Bora et al conducted research using the eyes test and the hinting task, aiming to investigate the theory of mind deficits in euthymic patients and how other cognitive impairments are engaged with those deficits. They found that even the bipolar disorder patients in remission could exhibit deficits in theory of mind which is impacting social functioning in a negative way. They also showed theory of mind impairments are in relation with various cognitive deficits such as impaired executive functioning and impairments in emotion recognition.

2.2.4 Impact of Social Cognition Deficits in Borderline Personality Disorder

Another disorder that has a social cognitive part is the borderline personality disorder. Borderline personality disorder is characterized as the disturbed affective, cognitive, behavioral, and interpersonal symptoms. Resulting in unstable self image and personal relationships (APA, 2013). A recent study by Baez et al. (2015) exhibited that the patients with borderline personality disorder have difficulties in theory of mind and also emotion cognition. Their executive functioning is also affected by the complexity of the tasks such as their theory of mind performance. They have been found to perform poorly in the tasks involved real life scenarios and required the incorporation of contextual cues. They showed lower performance on the false belief tasks while not showing lower performance on the task requiring the reading of the eyes, therefore the researchers suggest that the borderline personality disorder patients show decreased theory of mind skills in the tasks involving real life social interactions. Also the study by Zabizadeh et al. (2017) explored the relationship between borderline personality disorder and theory of mind. They found that the performance of the borderline personality disorder patients depend on the aspects of the theory of mind task. For the affective theory of mind tasks, the patients with the borderline personality disorder had performed better from the healthy control group. However, for the cognitive theory of mind tasks, they have performed worse than the healthy control groups. The borderline personality disorder patients with also major depression disorder had overall decreased theory of mind skills. In 2018, Nemeth et al. conducted a meta-analysis on the theory of mind and borderline personality disorder, finding evidence that the borderline personality disorder patients exhibit distinct impairments in ToM. They especially struggle more with the tasks requiring mental state reasoning using cognitive methods. Their analysis also showed that as the task complexity increased, also the impairment of theory of mind in individuals with BPD became more evident.

2.2.5 Impact of Social Cognition Deficits in Major Depressive Disorder

In 2016, Bora and Berk conducted a meta-analysis to investigate theory of mind (ToM) abilities in individuals with major depressive disorder (MDD) compared to healthy controls. Their aim was to determine the interaction between MDD and TOM and to what extent they were affecting each other. Their meta-analysis included 18 studies comparing 613 patients with MDD and 529 healthy controls. Their research showed that there are notable ToM deficiencies in MDD patients. The level of the depressive symptoms were the extent that the impairment was associated. They also showed that the impairments existed even if they used an affective theory of mind task or cognitive theory of mind task. Their study concluded that ToM deficiencies in MDD are significant and might take part in the social and functional struggles experienced by individuals with depression.

2.2.6 Impact of Social Cognition Deficits in Social Anxiety Disorder

Social anxiety disorder (SAD) also involves impairments in social cognition, as it is characterized as a marked fear or anxiety about one or more social situations in which the individual is exposed to possible scrutiny by others according to the American Psychiatric Association (2013). They have a fear of being negatively evaluated and therefore they show anxiety symptoms. In 2014, Hezel&McNally did research investigating the theory of mind impairments in the individuals with social anxiety disorder (SAD). They found that the individuals with SAD performed worse on the theory of mind tasks compared to the non anxious control group. They were more prone to the errors in attribution of excessive feelings and intentions to other people. Their findings suggest that individuals with SAD may misinterpret social cues by overanalyzing others' mental states.

2.3 The Cerebellum’s Role In Neuropsychiatric Disorders: Social Cognition and Emotional Regulation

It is well known that the cerebellum has cognitive and limbic parts (Schmahmann et al., 2007), and there is consensus that the cerebellum is part of the social cognitive brain network (Van Overwalle, F., Manto, M., Cattaneo, Z. et al., 2020). If the cognitive cerebellum, posterolateral regions and the dentate nuclei, gets damaged, we face cerebellar cognitive affective syndrome, which is the Schmahmann syndrome (Schmahmann, 1998). If the damage is on the limbic parts of the cerebellum, vermis and fastigial nuclei, then it leads to the neuropsychiatric disorders. One of the first suggestions on the cerebellar roles in neuropsychiatric disorders was made by Hamilton et. al in 1983. They investigated three patients who had major depressive disorder, schizophrenia and bipolar personality disorder. Each of the patients had cerebellar lesions, which made the researcher come to a suggestion as the cerebellum might be closely related to the disorders. In the consensus paper of Van Overwalle et al. (2020) their results emphasize that the cerebellum plays a significant role in social cognition and they provide evidence that cerebellar dysfunction is linked to various neuropsychiatric disorders, such as autism spectrum disorder (ASD), schizophrenia, bipolar disorder, and major depressive disorder. In 2013, Ecker and colleagues demonstrated that abnormalities in the cerebellar gray matter (GM) could serve as a key biomarker for distinguishing individuals with Autism Spectrum Disorder (ASD) from those who are typically developing. They highlighted that alongside with other regions, structural differences in the cerebellum also is identified as a neural underpinning of ASD. Additionally, an fMRI research by Olivito et al (2018) showed that adults with ASD exhibit distinct pattern of cerebellar changes in terms of both functional connection with cortical regions and morphometry, such as the size and the shape of the cerebellum and how it connects to the other brain areas. In 1979, Heath, Franklin, and Shraberg were among the first to suggest the cerebellum's role in schizophrenia and other functional psychoses. In their study, an important number of patients diagnosed with schizophrenia showed abnormalities in the cerebellar vermis and they highlighted that the cerebellum, especially the vermis is significant for the neurological and behavioral aspects of schizophrenia. A study by Katsetos, Hyde, and Herman (1997) provided strong evidence supporting Heath et al.'s (1979) research. In their study, Katsetos et al. (1997) showed the abnormalities in the cerebellum, especially in the vermis, contributed to the cognitive and perceptual impairments associated with schizophrenia. These abnormalities include a reduction in Purkinje cells and disruptions in the cerebellar-cortical feedback loop. In 2008, Andreasen and Pierson reviewed the existing evidence of the cerebellar involvement in schizophrenia and they confirmed the existing findings by showing as the Purkinje cell size reduced and there are disruptions in the cortico-cerebellar-thalamic-cortical circuit, the cerebellum is playing a significant role.

The cerebellar impairments, especially the impairments in the vermis and posterior lobe (VI, crus I, crus II, VII-IX) (Lupo et al., 2021) have a role in the affective symptoms of the bipolar personality disorder (Shinn et al., 2017; Lupo et al. 2021; as cited in Tai et al., 2024). The review highlighted that altered cerebro-cerebellar connectivity might play a crucial role in the pathophysiology of bipolar disorder, suggesting that the cerebellum's involvement in emotional and cognitive processing is significant (Shinn et al., 2017; as cited in Tai et al., 2024). Also Liang et al. (2022) researchers demonstrated that individuals with bipolar disorder had changes in how certain brain areas are connected during rest, particularly those involved in understanding others' emotions (cognitive empathy). These altered connections were weaker compared to healthy individuals, which might help explain why those with bipolar disorder often struggle with cognitive empathy. Compared to the healthy control group, the individuals with bipolar disorder had weaker connections, which could be an explanation why people with bipolar disorder frequently experience difficulties with cognitive empathy.

In the "cerebellar cognitive affective syndrome” studies of Schmahmann and Sherman (1998), they suggested that since the cerebellum has an important role in modulating higher-order cognitive and emotional functions, it could also be involved with borderline personality disorder (BPD). In 2016, De Vidovich et al. since there is evidence that the cerebellum takes part in Attention-Deficit/Hyperactivity Disorder (ADHD) (Roth and Saykin, 2004; De Vidovich et. al 2016) and schizophrenia (Andreasen and Pierson, 2008; De Vidovich et al., 2016) which impulsivity is one of the key symptoms, the cerebellum would be involved in borderline personality disorder as well, which also has increased impulsivity.

They tested their hypothesis with the repetitive transcranial magnetic stimulation (rTMS) on the left cerebellum and found significant improvement in cognitive performance in BPD patients, particularly in tasks requiring emotional and cognitive control. They showed that stimulation over the cerebellum can enhance the other brain areas involved in emotion regulation and impulsivity control, offering potential therapeutic benefits for BPD.

In a study by Talati (2013) researchers examined gray matter abnormalities in individuals with Social Anxiety Disorder (SAD) using magnetic resonance imaging (MRI) and voxel-based morphometry (VBM). They found that participants with SAD had significantly increased gray matter (GM) volume in the left cerebellum compared to healthy control subjects.

Depping et al (2018) investigated the role of the cerebellum in major depressive disorder (MDD) and they identified that patients with MDD often show changes in the cerebellum, particularly in lobule VIIA. They suggest that the engagement of the cerebellum in MDD goes beyond motor control, having an important role in the cognitive and emotional symptoms associated with the disorder.

With the provided studies and much more research, it is obvious that the cerebellum studies have a significant importance for the individuals who have neuropsychiatric conditions. With its dysfunction linked to a wide range of disorders, including schizophrenia, bipolar disorder, autism spectrum disorder (ASD), and major depressive disorder (MDD), social anxiety disorder (SAD), the cerebellum research is a critical point of the science world. The reviewed literature demonstrates how particular cerebellar regions, such as the vermis and posterior lobes, contribute to the pathophysiology of these conditions, impacting cognitive empathy, emotional regulation, and social cognition. In the therapy world, it would be beneficial to target cerebellar pathways since they might offer new avenues for treatment.

3. UNDERSTANDING THE CEREBELLUM AND ITS ROLES IN SOCIAL COGNITION

3.1 Key Milestones in the History of Cerebellar Neuroscience

It is well-known that the cerebellum plays crucial roles in cognitive abilities and social cognition, but the understanding of its functions took a slow start until the eighteenth century. It was based on observations, not very detailed per se, primarily gross anatomical. Even though studies about the cerebellum trace back to ancient times, it was not until recent times that it was known that the cerebellum is beyond memory and motor control functions (Rawson, 1932). Herophilus was a pioneer who identified the cerebellum as a critical organ. Right at our neck, there lies a fountain of nerves, in his words. This fountain is located in the posterior fossa of vertebrates (Ponce, Klaus, & Schutter, 2022) and we call this fountain the cerebellum. Herophilus was very influential; his light shone through Galen and Varolio, helping them gain insights about the cerebellum. These early scholars paved the way for centuries of cerebellar research (Rawson, 1932). Today, we owe a significant amount of our knowledge to the studies focusing on the damages to the cerebellum. An important percentage of them belong to the animal studies which was the beginning point of cerebellum research. Du Verney (1673) holds the distinction of being one of the earliest researchers to conduct groundbreaking animal studies. In his studies, he removed or damaged the cerebellum of pigeons and observed how their movement and motor control were affected, a method common among many researchers whom he influenced (Ponce, Klaus, & Schutter, 2022). Concurrently, Johannes Evangelista Purkinje became extremely famous for his work on the nerve cells composing the brain and the cerebellum, which were named after him, Purkinje cells (Sotelo, 2010). Meanwhile, Vincenzo Malacarne became the first researcher to publish work entirely dedicated to the cerebellum. He provided the initial comprehensive description of the cerebellum and the most accurate anatomical description made until the 18th century (Glickstein, Strata, & Voogd, 2009).

One other very important pioneer was Luigi Rolando, whose work on cerebellar lesions impaired movement and gained attention at the beginning of the 19th century (1773–1831). He was one of the first to use electricity to study cerebellar functions. His observations on galvanic currents revealed that the cerebellum elicited convulsions. Furthermore, his animal studies included goats whose cerebellums were removed, leading him to see that the animals couldn't move and theorizing that the cerebellum controls motor function through the transmission of nerve fluid (Voogd & Koehler, 2018; Rolando, 1809). He attributed this to his idea of the cerebellum producing the electrical impulses leading to movement (Coco & Perciavalle, 2015). In 1824, Flourens criticized Rolando (Coco & Perciavalle, 2015) and pursued research involving different animals, such as dogs and pigs, alongside studying pigeons. He observed that the animals could still move, albeit with incoordination of the movements. This investigation led him to discover the cerebellum's role in movement control, proposing a connection between cerebellar lesions and muscle incoordination (Manto & Haines, 2012). Malacarne's work gained the attention of Johann Christian Reil (1759–1813) and Karl Friedrich Burdach (1776–1847), and they employed alcohol fixation to validate and expand upon his depiction. Their work created the enduring terminology for cerebellar lobules, which is still valid to this day (Reil, 1807–1808; Burdach, 1819–1826; Glickstein, Strata, & Voogd, 2009).

The studies of Camillo Golgi (1873) provided one of the most significant leaps in understanding the complex structure of the central nervous system by developing a new way to stain and visualize nerve and macroglial cells (Sotelo, 2010). The technique he invented, called the black reaction, helped researchers reveal neurons with all their processes and was widely adopted in the research world, with Cajal as the prominent promoter (Pannese, 1999; Sotelo, 2010). The difference in Golgi and Cajal's approaches was that while Golgi thought axons merged into a single network, Cajal believed axons ended freely, without neuron communication. Cajal's approach focused on contiguity between neurons rather than continuity (Sotelo, 2010) and he ultimately unraveled the entirety of the cerebellar circuit. Thanks to his intense work, our understanding of the cerebellum had a foundation for further investigation. Golgi and Cajal jointly documented the details of the cerebellar cortex, leading them to share the Nobel Prize in 1906 (Sotelo, 2008).

3.1.2 Cerebellar Research in the 20th Century: Expanding Beyond Motor Control

In the early 20th century, Gordon Holmes conducted studies on cerebellar damage. He studied the lesions of World War I soldiers, with cerebellar damage from gunshot wounds revealing significant symptoms such as disturbances in muscle tone, irregularities in voluntary movements, and ataxia. These studies were particularly enlightening in understanding the functions of motor control and coordination (Holmes, 1917). Furthermore, Sir John Eccles’s studies advanced our understanding of neural communication and synaptic function within the brain. He identified the excitatory and inhibitory nature of various cell types, which, in turn, provided a comprehensive understanding of the cerebellar cortex. His studies earned him a Nobel Prize (Glickstein, Strata, & Voogd, 2009). Masao Ito (2006) refers to him as “he opened another neuroscience chapter”. Masao Ito researched long-term depression (LTD) in cerebellar functioning, demonstrating the cerebellum's intricate neural circuitry. He investigated the cerebellar roles not only in motor control but also in learning and memory mechanisms, as well as the cerebellum’s roles in higher cognitive functioning (Ito, 2006). Ito and Janos Szentágothai (1912–1994) concurrently studied the involvement of the cerebellum in higher cognitive functions after Leiner et al. (1986) proposed it. Leiner et al. also suggested the intensive connections of the cerebellar cortex with the cerebral cortex, prompting Ito to emphasize that the cerebellum has a unique structure. Imaging and modeling studies have tremendously supported this hypothesis, resulting in increased attention on the cognitive functions of the cerebellum (Ito, 2006).

A pivotal figure in the field who dedicated their attention to discovering the cerebellum's role in cognitive functioning was Jeremy D. Schmahmann. His theory, "dysmetria of thought," proposed that the cerebellum regulates cognitive processes. His research on cognition and emotion led him to coin the significant term "Cerebellar Cognitive Affective Syndrome" (CCAS), also referred to as Schmahmann syndrome, which focuses on cerebellar impairments (Schmahmann, Guell, Stoodley, & Halko, 2019). Schmahmann (1991) showed that impairments in the cerebellum lead to neuropsychiatric symptoms, emotional regulation issues, and behavioral changes.

Recent research has especially focused on the crucial role of the cerebellum in learning, social cognition, and emotion (Glickstein, Strata, & Voogd, 2009) showing that the cerebellum is involved in a wide range of neurological functions, with its unique existence and sprawling connections within the cerebral cortex (Schmahmann, Guell, Stoodley, & Halko, 2019). Nowadays, cerebellar research especially focuses more on how the cerebellum takes on the role of mentalizing. A seminal series of meta-analyses by Van Overwalle and colleagues (2014, 2015a) significantly advanced our understanding of the cerebellum's role in this high order cognitive ability. Their studies have highlighted the importance of the cerebellum as a part of the mentalizing areas, while emphasizing the cerebellum's many cognitive functions (Van Overwalle, Ma, & Heleven, 2020).

3.2 The Fountain Of The Nerves: Cerebellar Anatomy and Architecture

With its brain-like appearance, the cerebellum is an anatomically distinct structure (Stoodley & Schmahmann, 2018). It was influenced by natural selection more than other regions and underwent significant changes, expanding faster than the neocortex (Barton & Venditti, 2014). It weighs about 150 g, yet it is the largest part of the hindbrain. It is positioned posterior to the pons and medulla oblongata and separated from them by the fourth ventricle (Singh, 2021). Its unique architecture includes two hemispheres and three well-demarcated fissures and the hemispheres are connected by the midline vermis (Stoodley & Schmahmann, 2018). The cerebellar hemispheres (excluding the vermis and paravermis) are called the cerebrocerebellum (Unverdi & Alsayouri, 2023). The tentorium cerebelli divides the cerebellum from the cerebrum (Dekeyzer et al., 2023) and three pairs of cerebellar peduncles connect the cerebellum to the brainstem. These large bundles of fibers control the incoming and outgoing nerve paths, transmitting the efferent and afferent nerve tracts of the cerebellum (Sillitoe, Fu, & Watson, 2012, p. 363). These fiber tracts carry signals to and from the cerebellar nuclei (Kebschull et al., 2024). The superior peduncle connects to the midbrain, the middle to the pons, and the inferior peduncle to the medulla oblongata (Singh, 2021). These peduncles facilitate communication between the cerebellum and the rest of the central nervous system (Dekeyzer et al., 2023).

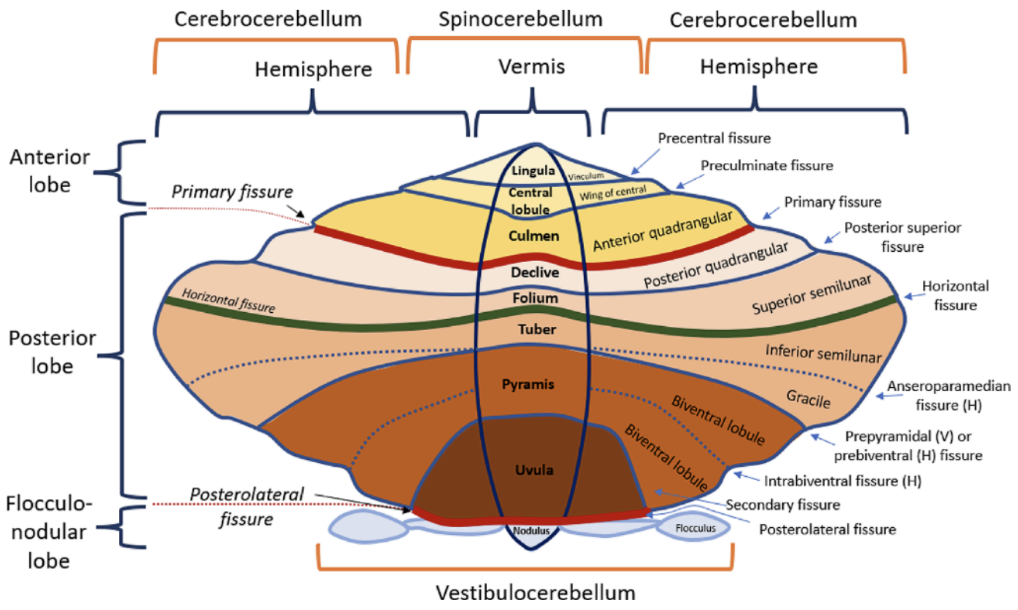


Figure 3; Major anatomical subdivisions of the cerebellum (Dekeyzer et al., 2023)

3.2.1 Cerebellar Lobes and Their Functions

There are 10 lobes in the cerebellum, and each of them plays a distinct role in cerebellar functioning (Leggio & Olivito, 2018). The cerebellum is divided into three primary lobes: the anterior lobe (lobules I-V), the posterior lobe (lobules VI-IX), and the flocculonodular lobe (lobule X) (Stoodley & Schmahmann, 2018). The lowest region of the cerebellum, known as the flocculonodular lobe (FL), is essential for balance and eye movement (Ozgen et al., 2024). The anterior lobe is in charge of motor control, as shown by Holmes (1917), with cerebellar motor syndromes arising from lesions of the anterior lobe. The third lobe, the posterior lobe, is in charge of cognitive-affective functioning and behavioral changes (Schmahmann & Sherman, 1998) and it is evolutionarily younger among all the others (Lent *et al.*, 2012). The posterior cerebellum is a part of the mentalizing/default network of the cerebellum (Buckner *et al.*, 2011) and recent evidence comes from Van Overwalle et al (2015a) who demonstrated that mentalizing processes are sub-served by the posterior cerebellum. Especially the Crus I and Crus II, the most significant and the key areas in the human cerebellum, have evolved to connect with the prefrontal cortex which is engaged in higher-order tasks (Balsters et al., 2010; Stoodley & Schmahmann, 2009).

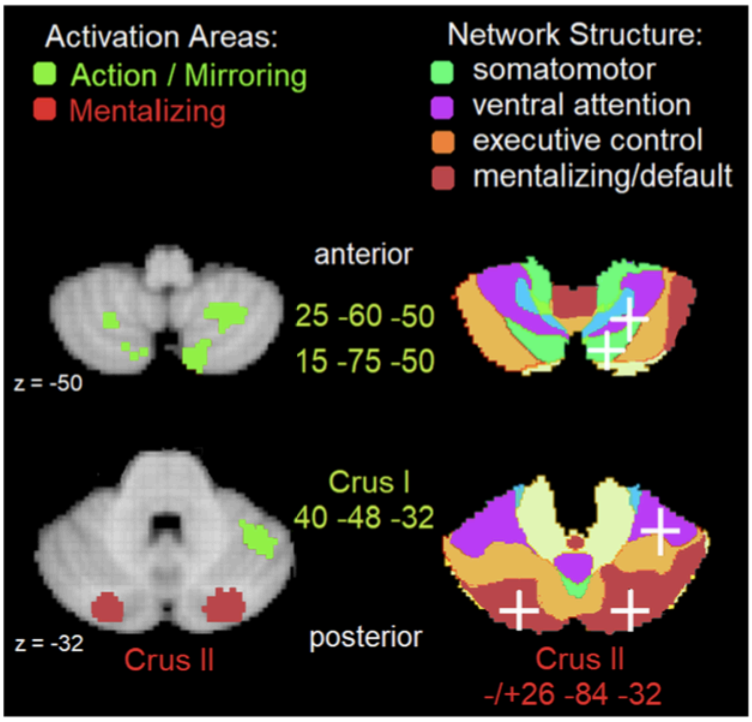


Figure 4; Mirror and Mentalizing Areas in the Cerebellum (Van Overwalle et al., 2020)

In the lobules, especially in the large lobules and small folds (folia), the cerebellum has a tightly folded nature. The neural tissue is thin, and the folded construction makes the cerebellum appear small. Despite the small size and two-dimensional structure of the cerebellum, it has a surface area of 1,590 cm^2, covering 78% of the human neocortex due to its extremely folded nature (Sereno et al., 2020). Around the nineteenth and twentieth centuries, studies of myelin and degeneration investigated the cerebellar connections with the spinal cord, vestibular system, brainstem, and cerebral cortex, showing that there is a topographic manner (Gruol et al., 2016). Data from neuroimaging and neuroanatomical studies support the research on cerebellar connections and steadily show the topographic organization between the cerebellum and the mentioned areas. As a result of this organization, the cerebellum has subregions in sensorimotor, association/cognitive, and limbic regions (Stoodley & Schmahmann, 2018). Schmahmann (1991) illustrated immense connections of the cerebellum with the posterior parietal and prefrontal cortical regions. The connections within the limbic cerebellum show the involvement of the cerebellum in emotional and affective behavior (Heath et al., 1977; Schmahmann, 1991). While three pairs of cerebellar peduncles directly connect the cerebellum to the brainstem, pathways involving dopamine, serotonin, and norepinephrine link the cerebellum to the brainstem regions. They play significant roles in mood regulation (Dempsey et al., 1983; Marcinkiewicz et al., 1989; as cited in Schmahmann, 1996). In contrast, output from the cerebellar nuclei is directed through the thalamus to the cerebrum (Habas et al., 2019). Traditionally, it is understood that the cerebello-thalamic projections originating from the three output nuclei primarily target the motor cortex (Nashef et al., 2019; Nashef et al., 2021).

3.2.2 Anatomical and Functional Organization of the Cerebellar Cortex

Research on the cerebellar cortex has a rich and extensive history. Jan Evangelista Purkyně (1787–1869) made a significant contribution in 1837 by identifying Purkinje cells. Santiago Ramón y Cajal's detailed descriptions of the neuronal structure of the cerebellar cortex provided a foundational understanding that has guided subsequent research (Ramón y Cajal, 1894; Ramón y Cajal, 1911; as cited in Albright et al., 2001). Their pioneering work established key concepts and terminology, such as mossy fibers, granular cells, parallel fibers, and climbing fibers, which remain relevant in current cerebellar research (Gruol et al., 2016).

The cerebellar cortex is organized into three layers: the superficial molecular layer, the Purkinje cell layer, and the granular layer (Sillitoe, Fu, & Watson, 2012). The molecular layer, the outermost layer, contains the dendrites of Purkinje cells and axons of granule cells. The Purkinje cell layer, situated beneath the molecular layer, is composed of the cell bodies of Purkinje cells. The granular layer, the innermost layer, surrounds the cerebellum's medullary center and is populated by granule cells, which are the most numerous in the cerebellar cortex, while Purkinje cells are the most prominent (Sillitoe, Fu, & Watson, 2012).

This well-organized structure features a central trisynaptic circuit involving mossy fibers (MFs), granule cells (GrCs), and Purkinje cells (PCs), along with local interneurons. Mossy fibers excite granule cells, which in turn excite Purkinje cells. Purkinje cells, large GABAergic neurons, serve as the sole output of the cerebellar cortex (Hull & Regehr, 2022; Voogd & Glickstein, 1998). Purkinje cells receive strong excitatory inputs from climbing fibers (CFs) and are inhibited by Golgi cells (GoCs) and molecular layer interneurons (MLIs) (Hull & Regehr, 2022). Mossy fibers and climbing fibers are major inputs to the cerebellar cortex. Mossy fibers, originating from the brainstem and spinal cord, indirectly innervate

Purkinje cells via granule cells. Together with climbing fibers, these inputs form the core of cerebellar cortical neuronal circuits (Takahashi & Shinoda, 2021). The axons of Purkinje cells extend to the deep cerebellar nuclei, from which efferent projections are sent to other brain regions (Kang et al., 2021).

3.2.3 Structural and Functional Overview of the Cerebellar Nuclei

The cerebellar nuclei are located deep in the cerebellar white matter and serve as the primary output centers of the cerebellum (Sillitoe, Fu, & Watson, 2012). Their structured architecture, coupled with intricate afferent and efferent connectivity, plays a crucial role in processing cerebellar cortex computations that impact behavior and other brain functions (Kebschull et al., 2024). Nearly all outputs from the cerebellum originate from these nuclei (Kebschull et al., 2024).

In human anatomy, the cerebellar nuclei consist of four main structures: the fastigial nucleus, the interposed nucleus (divided into emboliform and globose nuclei), and the dentate nucleus. The fastigial nucleus, the oldest and smallest among them, projects to the midline vermis (Zhang et al., 2016). The interposed nuclei project to the paramedian regions, while the dentate nucleus projects to the lateral hemispheres (Stoodley & Schmahmann, 2018). The fastigial nucleus primarily controls motor functions, but recent evidence suggests it also contributes to non-motor functions (Zhang et al., 2016). Küper et al. (2011) demonstrated that the interposed nucleus is involved in grip forces, prehension, and grasping movements. Additionally, Glickstein et al. (2011) highlighted the interposed nucleus's role in coordinating precise motor outputs and limb movements. The dentate nucleus, which receives inputs from the premotor cortex and supplementary motor cortex through corticocerebellar, pontocerebellar, and spinocerebellar tracts, plays a role in motor execution, visuomotor control, cognition, planning, initiation, and regulation of volitional movements (Akakin et al., 2014). Deep cerebellar nuclei also project to the ventral tegmental area (VTA). VTA and its dopaminergic neurons are recognized for the crucial involvement in reward and stress-related behaviors (Morales & Margolis, 2017; Russo & Nestler, 2013; Fox & Lobo, 2019; Kang, Jun et al., 2021). Recently, the advanced tracing methods that target both dopaminergic and GABAergic neurons have confirmed a monosynaptic link between the DCN and the VTA

(Beier et al., 2015; Carta et al., 2019; Kang, jun et al., 2021). The connections originate primarily from the dentate nucleus (DN).

3.2.4 Afferent and Efferent Pathways of the Cerebellum: Communication Mechanisms

To understand the cerebellum's variety of functions, it is crucial to grasp the intricate network of afferent and efferent pathways that facilitate communication between the cerebellum and other regions of the brain and spinal cord (Takahashi & Shinoda, 2021). For cerebellum to process the sensory information and coordinate motor outputs and also making the precise movements smoother, these circuits are essential. Communication between the cerebellum and the contralateral cerebrum relies on these two polysynaptic circuits. The afferent pathways are in charge of carrying the information to the cerebellum from the pons, various parts of the brain, and the spinal cord (Kebschull et al., 2024) in other words, they are responsible for the sensory and proprioceptive information transfer. They convey real-time information about the body's posture, movement, and surrounding environment to the cerebellum which is necessary for the cerebellum to maintain posture and balance while dynamically adjusting motor activities. On the other hand, the efferent pathways are the primary routes through which the cerebellum sends its outputs to other parts of the brain and spinal cord. The efferent pathways project from the cerebellum to the deep cerebellar nuclei, which serve as relay stations, and to the cerebral cortex (Evarts & Thach, 1969; Kemp & Powell, 1971; Strick, 1985; Schmahmann & Pandya, 1997, as cited in Buckner, 2013). These pathways are crucial for motor functioning and behavior (Kebschull et al., 2024), in which the cerebellum modifies the activity of both motor and non-motor brain regions to influence voluntary motions, motor learning, and even cognitive functions.

These two pathways work in coordination for the cerebellum to connect sensory information with motor commands and contribute to the ensuring smooth and precise movements. This coordination also contributes to cognitive functions. Disruptions in these pathways can lead to significant motor and cognitive deficits, underscoring their critical role in cerebellar functionality. These pathways are crucial for the functioning of the cerebellum and their disruptions can lead to motor and cognitive deficits (De Benedictis et al., 2022).

3.2.5 Cerebro-Cerebellar Connectivity: Mapping Pathways and Interactions

The connections between the cerebral cortex and cerebellum are numerous (Ito, 1984), leading the cerebellum to be involved in processes beyond motor control and significantly affecting overall brain dynamics (Palesi et al., 2020). The cerebro-cerebellar circuits form the foundation for the cerebellum's roles, particularly in non-motor functions (Botez et al., 1985, as cited in Kelly & Strick, 2003). Advanced tractography techniques have enabled the re-establishment of tracts between the cerebellum and cerebral cortex, revealing associative regions along cerebro-cerebellar loops (Palesi et al., 2015, 2017b; Palesi et al., 2020). For the first time, Palesi et al. (2020) used The Virtual Brain model to demonstrate that cerebro-cerebellar connections play a crucial role in shaping whole-brain dynamics. Additionally, the cerebellum contributes to higher-order processing through these cerebro-cerebellar connections (Boven & Cerminara, 2023). Studies also show that the cerebellum plays a significant role in driving cerebral activities related to goal-directed behavior (Dacre et al., 2021; Boven & Cerminara, 2023).

The cerebellum can be functionally divided into three zones: the vestibulocerebellum, the spinocerebellum, and the cerebrocerebellum (Dekeyzer, Vanden Bossche, & De Cocker, 2023). The vestibulocerebellum, which includes the flocculonodular lobe, is the most ancient part and is involved in regulating eye movements and balance. The spinocerebellum is responsible for muscle movements and motion abnormalities, receiving information directly from the spinal cord. The cerebrocerebellum, the most recent evolutionary development, receives input from the cerebral cortical areas (Dekeyzer, Vanden Bossche, & De Cocker, 2023). Cerebro-cerebellar circuits provide a bidirectional connection between the cerebellum and the cerebrum (Watson et al., 2013). In the mid-1980s, the advent of human neuroimaging techniques revolutionized the indirect mapping of brain function (Raichle, 1987, as cited in Buckner, 2013). Notable reviews by Henrietta Leiner, Alan Leiner, and Robert Dow set a foundational understanding of the cerebellum’s connections with cerebral association regions (Leiner et al., 1986, as cited in Buckner, 2013). The cerebellum-cerebrum loop is recognized as one of the most significant and evolutionarily advanced circuits in the brain (Rilling & Insel, 1998; Sultan, 2002; Herculano-Houzel, 2010; as cited in Boven & Cerminara, 2023).

3.3 The Cerebellum’s Diverse Roles: Motor Control and Beyond

3.3.1 Cerebellum’s Roles in Motor Control and Movement Coordination

Galen (2nd century CE) speculated that the cerebellum was the origin of the spinal cord and motor nerves, reflecting early ideas about its role in controlling movement and transmitting nerve signals (Clarke & O'Malley, 1996; Morton & Bastian, 2004). Since the pioneering work of Rolando (1773–1831) and Flourens (1824) on animal lesion studies, it has been well established that the cerebellum plays a crucial role in controlling motor activities. Their research laid the foundation for understanding the cerebellum's involvement in motor function, demonstrating that lesions in this area lead to significant impairments in movement ability. Flourens, in particular, highlighted the cerebellum's essential role in coordinating voluntary movements, a finding that has since been supported by numerous animal studies showing that cerebellar damage disrupts motor coordination and execution. Early studies of patients with gunshot wounds, Friedreich's ataxia, and cerebellar cortical atrophy (Brown, 1892; Marie, 1893; Babinski, 1899; Holmes, 1907) have also shown the critical role the cerebellum plays in coordinating limb movements. These studies further demonstrate the involvement of the cerebellum in coordination by demonstrating its roles in walking, posture, balance, and speaking (Gruol et al., 2016). As the field of neurology evolved from the nineteenth into the twentieth century, leading researchers like Joseph Babinski and Gordon Holmes advanced our understanding of the cerebellum's role in motor control. They demonstrated that damage specifically to the cerebellum impairs various motor functions, including coordination, speech production, and eye movements. This was a significant shift from earlier views and highlighted the cerebellum's critical involvement in these motor processes (Babinski, 1902; Holmes, 2007; Salman & Tsai, 2016).

The cerebellum helps control and coordinate movements by interacting with two key brain areas: the motor cortex and the brainstem's motor circuits. By accessing the motor cortex and brainstem, the cerebellum regulates movement. It sends extensive neural signals to the ventrolateral thalamus, a crucial relay station in the brain, through the output regions. Once the cerebellum sends signals to the ventrolateral thalamus, individual neurons within the thalamus transmit these signals over extensive pathways to the primary motor cortex (Shinoda et al., 1993). This process helps the motor cortex coordinate and integrate muscle movements across different body parts, ensuring that both timing and spatial aspects of these movements are synchronized. This coordination is essential for executing precise and well-orchestrated motor actions, highlighting the thalamus's role as a key relay station in the brain's motor control system (Shinoda et al., 1993). When it comes to controlling and coordinating movement, both the cerebellum and basal ganglia are essential. Damage to either of these areas can lead to distinct motor impairments. For instance, issues with the basal ganglia may result in symptoms like tremor (involuntary shaking), rigidity (muscle stiffness), and akinesia (difficulty initiating movement) (Middleton & Strick, 2000). Ackermann and Ziegler (1991) have also shown the cerebellum's role in rhythmic oscillations (tremors) in both speech and posture. Rueckriegel et al. (2009) found that the patients with the cerebellar tumors go through substantial impairments in fine motor skills. They had a hard time completing intricate tasks like writing sentences or drawing circles. These findings were related to ataxia. Rueckriegel et al. (2009) highlighted that treating fine motor dysfunctions in patients is crucial for their everyday lives, since these issues might have a significant impact on their quality of life.

3.3.2 The Cerebellum's Role in Learning and Memory

Functional brain imaging methods kept enhancing our knowledge of brain–behavior relationships and providing hypotheses about cerebellar computations and their locations that can be tested through patient studies. These studies have provided diverse roles of the cerebellum beyond motor control. One of the areas of interest is the cerebellar roles in memory and learning, such as working memory, implicit memory, and explicit memory (Desmond & Fiez, 1998). The cerebrocerebellar circuits make the cerebellum have a role in learning and automaticity (Schmahmann, 1997). Working memory can be summarized as the ability to maintain and manipulate information in real-time, involving a central executive process, which acts like a manager, coordinating and controlling different mental tasks. When it comes to verbal information such as letters, words, or numbers, we use a silent rehearsal strategy. We can retain the information in our minds by using a technique called silent repetition, which works similarly to how our speech muscles work when we speak aloud (Baddeley, 1992; Desmond & Fiez, 1998). This would also include learning processes. The studies have looked into how the cerebellum works with the complexity of the working memory tasks (Marvel & Desmond, 2010). Pezzulo (2013;Koziol et al., 2014) suggests the role of the cerebellum is to enable the transformation of procedural learning, which transforms declarative knowledge through internal model development, meaning that the cerebellum is facilitating complex cognitive tasks. Yamazaki (2012;Koziol et al., 2014) also agrees with Pezzulo and says procedural learning mediated by the cerebellum encourages the formation of declarative knowledge and conscious control. When the working memory demands are complex and high, this cerebellar facilitation of the organization and regulation plays a critical role in preserving knowledge of internal linguistic processes that promote memory retention and cognitive activities (Koziol et al., 2014).

One of the first studies to show the cerebellum’s crucial role in verbal working memory and covert articulation was done by Paulesu et al. (1993). Together with the left frontal operculum and supplementary motor area (SMA), the cerebellum was significantly more active during verbal tasks. Similar results were shown by Awh et al. (1996). They exhibited cerebellar activation during tasks that require the maintenance of verbal information. (Fiez & Raichle, 1997) noted that the cerebellum is involved in tasks requiring the silent rehearsal of verbal items, known as covert articulation. This emphasizes its role in creating internal articulatory representations, which are crucial for memory and cognitive processes. All of these results point to the cerebellum's important involvement in a variety of working memory-dependent cognitive functions (Fiez & Raichle, 1997).

3.3.3 Cerebellum as an Internal Clock

The human cerebellum acts as an internal clock for movement control. One of the first studies on this matter was done by Richard Ivry (1993), focusing on cerebellar lesions. His research on timing has focused on two primary tasks. The first was a production of time task, where participants perform a repetitive finger-tapping task. Initially, subjects had to synchronize their taps with computer-generated tones. After the tones stop, they had to continue tapping at the target rate for 30 unpaced intertap intervals (ITIs). The variability in the standard deviation of ITIs is the key measure, reflecting the task's requirement for explicit timing control. The second task involved perceiving time, where participants compare two intervals: a standard and a comparison interval. The goal was to determine whether the comparison interval is shorter or longer than the standard one. By varying the duration of the comparison interval and analyzing responses, researchers estimate the difference threshold to gauge temporal acuity. His study showed that disruptions or lesions in the cerebellum led to significant difficulties in maintaining accurate timing, highlighting the cerebellum's key role in regulating and adjusting temporal intervals (Ivry, 1993). After his study, the cerebellum's crucial role in the timing and sequencing of movements was recognized. Damage to the cerebellum can manifest as ataxia, a condition meaning "without order," which highlights its role in movement coordination and sequencing. Ataxia includes characteristics such as movement decomposition, intention tremor, dysmetria, and dysdiadochokinesis (Trouillas et al., 1997; Spencer & Ivry, 2013). Temporal disturbances in ataxia can present as hypermetria, where movements are faster than intended (Flament & Hore, 1986; Spencer & Ivry, 2013), or dysdiadochokinesis, where a person struggles with rapid, alternating movements (Day et al., 1998; Spencer & Ivry, 2013). Researchers have used tapping tasks to investigate the cerebellum's role in timing. In these tasks, participants synchronize their movements with a metronome, typically by tapping a finger. Those with cerebellar lesions show a significant increase in movement variability during repeated tapping (Franz et al., 1996; Ivry & Keele, 1989; Spencer et al., 2003; Spencer & Ivry, 2013). A study by Théoret, Haque, and Pascual-Leone applied 1 Hz repetitive transcranial magnetic stimulation (rTMS) to the medial cerebellum for 5 minutes and found increased variability in performance on the paced-finger-tapping task, with no effects on the lateral cerebellum or motor cortex. This study was among the first to demonstrate that rTMS can transiently disrupt cerebellar function and influence behavior (Théoret, Haque, & Pascual-Leone, 2001). Together, these studies underscore the cerebellum's essential role as an internal clock, crucial for the precise timing and sequencing of movements.

3.3.4 Cerebellum and Eye Movement Control

We have known that the cerebellum is involved in oculomotor control ever since Gordon Holmes began studying troops who had impaired eye movement due to cerebellar impairment brought on by the First World War (Prsa & Thier, 2022). All kinds of gaze fixation and eye movements are mediated by the cerebellum. Our understanding of this matter comes from neurophysiological data and studies on primates with cerebellar lesions (Manto et al., 2012). The vestibulocerebellum and the oculomotor cerebellum are two major anatomical subdivisions of the cerebellum that are primarily responsible for controlling distinct classes of eye movements. In 1976, Ritchie conducted research on cerebellar lesions in monkeys. His study revealed that damage to the cerebellum significantly impairs the accuracy and timing of saccadic eye movements. He removed the cerebellar cortex areas related to saccades, which in turn resulted in dysmetria, meaning that the eye movements became inaccurate. This was early proof of the cerebellum's important role in eye movement control, especially in the saccadic duration. His research also showed how the cerebellum is involved in maintaining stability in vision and coordinating fast eye movements. His research paved the path for a more comprehensive comprehension of cerebellar function in the regulation of movement (Ritchie, 1976). Noda and Fujikado (1987) investigated how the cerebellum's posterior vermis regulates monkeys' fast eye movements. Their results demonstrated the importance of Purkinje cells in lobule VII for these movements and how their absence reduced the capacity to elicit saccades, underscoring the function of these cells in regulating eye movements. With our knowledge about the cerebro-cerebellar connections expanding, research on the cerebellar conditions in eye movements also gained more ways to be studied. A functional anatomy study was carried out in 2000 by Nobre et al. to examine the connection between the execution of saccadic eye movements and the covert orienting of visual spatial attention. They also found cerebellar contributions to the eye movements. In 2005, Nitschke et al. used fMRI to further investigate how the cerebellum coordinates eye and hand movements. They showed different parts of the cerebellum were involved in different activations. Visually guided saccades activated the cerebellar vermis, while complex saccades and sequential hand movements activated additional regions in the cerebellar hemispheres and lobuli IV–VIII. Collectively, research demonstrates that the cerebellum is crucial for controlling eye movements and maintaining visual stability, from basic gaze fixation to complex saccades.

3.3.5 Cerebellar Roles In Emotion Processing

Although it seems like he research focusing on affective and emotional roles of the cerebellum only recently, the emotional roles of the cerebellum were an area of interest since Franz Joseph Gall (1758–1828), with him calling the cerebellum the seat of ‘amative love’ (Neuburger, 1897; Macklis & Macklis, 1992; Schmahmann, 2007). For the last couple of decades, researchers have started to seriously consider the role of the cerebellum in emotional regulation (Schmahmann, 2007). A study by Imaizumi et al. (1997) used PET to explore the neural correlates of identifying speaker identity and emotions from spoken words. The emotions were surprise, disgust, happiness, and anger. The participants had to identify the emotions of the speakers. To identify the speakers and link the vocal attributes with visual representations, the temporal regions and parieto-occipital junction were recruited. To identify the emotion, however, the noteworthy activation was on the cerebellum, the left middle frontal gyrus, and the right inferior frontal gyrus. This finding showed the cerebellum's role in processing emotional content. With the technological developments and lesion studies gaining more attention over the past decades, our knowledge of the emotional cerebellum has expanded from clinical, experimental, neuroimaging, and neurophysiological investigations (Adamaszek, D'Agata, & Ferrucci, 2017). With consistent research results showing the engagement of the cerebellum, it can be said that it is an important part of the network underpinning the ability to process emotional stimuli. Schmahmann and Sherman (2009) showed that the cerebellum has a critical role in emotional processing in their fundamental meta-analysis paper. The posterior vermis, known as the "limbic cerebellum," and regions like lobules VI and Crus I are key areas involved in this role. The tasks that involve empathy, sadness, and other emotional responses, particularly when processing negative stimuli, require the cerebellum. The different areas were involved in various information domains, and their study was important for anatomical, physiological, and clinical studies.

In their consensus paper, Adamaszek et al. (2017) also identify the cerebellum as an essential part of the limbic network and emphasize that especially the Crus I and Crus II regions are key regions in emotion perception. The cerebellum exhibits extensive connections (particularly of the vermis and fastigial nucleus) with the cortical and subcortical areas within the limbic system and takes roles in both experiencing and recognizing emotions (Blatt, Oblak, & Schmahmann, 2013). Baumann and Mattingley (2012) suggested a distinction between cerebellar subregions in processing different emotions, specifically in response to positive and negative emotionally relevant stimuli. The cerebellum is activated when we experience panic (Reiman et al., 1998), sadness, grief (Lane et al., 1997; Beauregard et al., 1998; Gundel et al., 2003), and pain (Becerra et al., 1999; Singer et al., 2004; Borsook et al., 2007; Leggio & Olivito, 2018). One interesting finding was by Singer et al. (2004). The activation of the cerebellum was different if the participants processed their own painful experience or another person's pain. If the participant was processing their own pain, the activation was in the posterior cerebellar vermis. If the participants were experiencing empathy for another's pain, the activated part was the posterior cerebellar hemisphere (lobule VI). They also showed that alongside the cerebellum, the anterior insula (AI) and rostral anterior cingulate cortex (ACC), which are the regions of the brain involved in the emotional aspects of the pain experience, were involved in experiencing our own pain or observing a loved one being in pain, while the somatosensory cortex only activated during self-experienced pain. It can be said that empathy engages the emotional aspects of pain, and the cerebellum is engaged in a neural network responsible for the processing of emotional aspects of empathy-related experiences (Singer et al., 2004).

A transcranial direct current stimulation (tDCS) study conducted by Ferrucci et al. (2012) found that (tDCS) over the cerebellum improved the recognition of negative emotions in facial expressions, specifically anger and sadness. Their research demonstrated how the cerebellum processes negative emotional stimuli and suggested that it is part of a neuronal network that also contains the amygdala and other regions associated with emotion. In 2021, Ferrari et al. found similar results supporting the recognition of negative stimuli. They demonstrated that the posterolateral region of the left cerebellum plays a role in influencing the activity of the motor cortex in response to negative emotional stimuli. Particularly when negative emotions are present, the posterolateral left cerebellum serves as a bridge, assisting in the integration and coordination of emotional events with physical and cognitive processing. Continued research conducted over the past few decades has demonstrated that specific cerebellar regions, particularly Crus I, Crus II, and lobule VI, are actively engaged in the perception of emotional expressions (Keren-Happuch, Chen, Ho, & Desmond, 2014; Stoodley & Schmahmann, 2009; Ferrari, Ciricugno, Arioli, & Cattaneo, 2023). The interconnections between the cerebellum and the prefrontal, temporal, cingulate, and posterior parietal cortices are the loops in which the cerebellum has its important role. When the connections with the brainstem are added, the cerebellum also becomes crucial in the complex interaction of neurotransmitters, such as norepinephrine, serotonin, and dopamine. Through this information, it can be said that the cerebellum is also involved in mood regulation in humans as well as emotion (Flace et al., 2021; Lanore et al., 2019; Saitow et al., 2013). A study conducted by Oostland & Hooft (2013) also demonstrated that serotonin levels in the cerebellum significantly influence mood regulation, as well as cognitive functions such as memory and learning. A meta-analysis of 80 neuroimaging studies with 2761 participants by Pierce et al. (2023) explored the cerebellum's role in processing emotions. In their study, they used both explicit emotional processing tasks and implicit emotion processing tasks. For the explicit tasks, the participants had to focus on the emotions, while in the implicit tasks, emotional processing occurred without direct awareness. They exhibited that the bilateral lobule VI, Crus I, and Crus II were involved during both tasks. They showed that the cerebellum's engagement in emotional processing is not dependent on conscious awareness. Malatesta et al. (2024) used cerebellar transcranial random-noise stimulation (ctRNS) to investigate the involvement of the posterior cerebellum in the perception and prediction of dynamic emotional expressions. They conducted an emotion discrimination task and found that ctRNS impaired the recognition of static sad expressions but enhanced the accuracy of recognizing dynamic sad expressions. Their study showed that the posterior cerebellum is not only involved in perceiving negative emotions but also plays a dynamic role in adapting to and predicting changes in emotional expressions over time.

3.4 The Cerebellum and Cognitive Processes: A New Understanding

Schmahmann was a pioneer in researching the cerebellum's involvement in cognition. He hypothesized that the cerebellum might play a role in cognitive processes. In 1985, Schmahmann consulted Sir John Eccles (1903–1997), who had conducted extensive studies on the cerebellum and asked Eccles, "Could the cerebellum play a role in cognition?". At that time, it was uncommon to consider the cerebellum is involved in cognition, as most research focused on its motor control functions. Sir John Eccles responded that he did not think so. After discussing the issue with another prominent scientist, Richard Thompson, Schmahmann learned about the work of Alan and Henrietta Leiner, as well as Robert Dow, who were investigating the cerebellum's potential cognitive roles. This led Schmahmann and his colleagues to hypothesize that association areas in the parietal, frontal, temporal, and limbic cortices transmit multimodal information with motivational and affective significance to the pontine nuclei. They proposed that the cerebellum modulates higher-order, behaviorally significant information in domains such as attention, executive function, language, emotion, and visual-spatial cognition—key elements of its functional influence (Schmahmann, 2010).

Furthering his research, Schmahmann encountered several key patients with cognitive and emotional impairments alongside cerebellar dysfunctions and tumors. These observations challenged the traditional view of the cerebellum as solely a motor control center and led to an investigation of its non-motor roles. Schmahmann developed the "dysmetria of thought" hypothesis and identified the Cerebellar Cognitive Affective Syndrome (CCAS). Patients with CCAS, particularly those with bilateral or posterior lobe lesions, experience difficulties in executive functioning, visual-spatial organization, personality alterations, and language difficulties (Schmahmann & Sherman, 1998).

CCAS suggests that the cerebellum is involved in cognitive and emotional processes, extending its recognized function beyond motor control (Schmahmann, 2010). In 1998, Schmahmann and Sherman conducted a study on the effects of cerebellar injuries on cognition and behavior. They examined 20 patients over a period of 7 years, all of whom had isolated cerebellar pathology. Through comprehensive neurological exams and neuroimaging, they identified a pattern of cognitive and affective dysfunctions, which is now known as "Cerebellar Cognitive Affective Syndrome" (Schmahmann & Sherman, 1998). Their findings highlighted the cerebellum's significant role in higher-order functions.

In a study on linguistic capabilities, Guell, Hoche, and Schmahmann (2015) compared 44 patients with cerebellar lesions to 40 healthy controls. They found that patients with cerebellar lesions exhibited significant impairments in higher-level metalinguistic abilities, such as interpreting ambiguities, making inferences, constructing meaningful sentences, and understanding figurative language. Their findings supported the "dysmetria of thought" theory, which posits that cerebellar dysfunction impairs cognitive processes in a manner analogous to its impact on motor control (Guell, Hoche, & Schmahmann, 2015). These studies, along with subsequent research, have established that the cerebellum plays a crucial role in cognitive functions.

The prominent scientists conducted pioneering research on the roles of cerebellum in cognitive functions. Adamaszek et al (2017) and Van Overwalle et al (2020) both exhibit results that the cerebellum is a key region mediating both social thinking and sensory-affective processes that are important in understanding what other people are thinking (Ferrari et al., 2023). In fact, during theory of mind (Van Overwalle et al., 2014) and emotion perception tasks, such as the identification of emotional faces (Fusar-Poli et al., 2009), the posterior cerebellum systematically activates. As a result, people with cerebellar impairments have trouble interpreting the emotions of others based on their voice or facial expression (Adamaszek et al., 2014; Hoche et al., 2016; Clausi et al., 2021a; Ferrari et al.,2023). Furthermore, research on neurostimulation has consistently demonstrated that tampering with posterior cerebellar activity impacts the capacity of healthy persons to discern the emotions of others based on their facial and body language (Ferrucci et al., 2012; Ferrari et al., 2023).

3.5 Cerebellum As A Part of the Social Brain

In addition to exploring the mirror neuron system and social brain, studies by Van Overwalle et al. (2014, 2019) have also identified the cerebellum as a crucial component of the social brain. A pioneering study by Ciricugno, Ferrari, Battelli, and Cattaneo (2024) investigated the cerebellum's role in social situations. They aimed to determine when the cerebellum contributes to social processing. Using chronometric transcranial magnetic stimulation (TMS), they examined the causal contribution of the posterior cerebellum to social processing and demonstrated that the cerebellum is involved at the onset of emotional processing. Their study also revealed that recruitment of the posterior superior temporal sulcus (pSTS) is dependent on the cerebellum, indicating that the cerebellum is a key node in the social brain network. Their findings underscore the importance of the cerebellum in social cognition. It is now well established that the cerebellum plays a role in non-motor processes, and its involvement in social cognition has gained increased attention in recent years (Schmahmann et al., 1998). The extensive connections of the cerebellum with regions that are involved in affective regulation, mood and higher cognition are providing support for the cerebellum's roles in emotional processes. The animal studies have also been showing these extensive connections with hypothalamus, septum, amygdala, insula, basal ganglia, as well as the neocortex and brainstem nuclei, which are the brain areas related to affective regulation and higher cognition (Anand et al., 1959; Middleton and Strick, 2001; Schmahmann, 2001; Schutter and van Honk, 2005; Snider and Maiti, 1976; as cited in Baumann&Jason, 2012).

3.5.1 The Default Mode Network and the Cerebellum: Interconnected Roles in Social Cognition and Mentalizing

One of the most important aims of cognitive neuroscience is to gain insight into the physical foundations of cognition. Neuroimaging studies have helped scientists throughout this journey of understanding the substrates of cognition, and a significant discovery was the exploration of the Default Mode Network (DMN) (Smallwood et al., 2021). Evidence for the network was seen while researchers were investigating brain activity during undirected mental states (Buckner et al., 2008). The human brain remains active even when we are not performing a specific task. Several brain regions can be seen to be active in human participants while they are not performing any particular activity (Shulman et al., 1997).

Collectively, this set of regions is now commonly referred to as the “default mode network” (DMN; Raichle et al., 2001; Buckner et al., 2008).

The default network also increases activity during mental explorations related to oneself, including remembering, speculating about potential social interactions, and reflecting on one's own future. The default network functions allow adaptive mental investigations, facilitating preparation for upcoming, personally significant events before they occur (Buckner et al., 2008). Imaging studies showed that the posterior cingulate cortex (PCC), medial prefrontal cortex (MPFC), and inferior parietal lobule (IPL) displayed constant activation during passive task conditions compared to goal-directed task performance, leading to the identification of the default mode network (Shulman et al., 1997; Raichle et al., 2001). When performing attention-demanding tasks, the DMN is normally suppressed; however, it becomes active during rest intervals (Raichle et al., 2001; Greicius et al., 2003). A study by Greicius et al. (2003) investigated the default mode network (DMN) in the human brain and confirmed the existence of the DMN by examining the connectivity of the posterior cingulate cortex (PCC) and the ventral anterior cingulate cortex (vACC). They showed strong coupling between these regions and other areas implicated in the DMN, such as the medial prefrontal cortex (MPFC) and inferior parietal cortex (IPC). The PCC showed significant resting-state connectivity with several regions, including the MPFC, left and right IPC, left dorsolateral prefrontal cortex (DLPFC), left inferolateral temporal cortex (ITC), and left parahippocampal gyrus (PHG) (Greicius et al., 2003). The DMN plays a role in social cognitive functions and shows increased activity during a variety of complex cognitive processes, including memory and abstract reasoning (Smallwood et al., 2021). Specifically, the anterior default mode network (i.e., the mPFC) is involved in self-referential thought and evaluating the past to plan for the future, while the posterior DMN (i.e., the PCC/precuneus) is involved in episodic memory, consciousness, and awareness (Andrews-Hanna et al., 2014; Sheline et al., 2009; Chen & Zhao, 2019). The default and somatomotor networks have a substantial overlap with the cerebellar regions engaged in social cognition during mind and body reading (Buckner et al., 2011; see also Buckner, 2013; Van Overwalle & Mariën, 2016). Studies have focused on the cerebellar zones interconnected with the default mode network (Buckner et al., 2008), and findings have shown that the bilateral Crus I, Crus II, and lobule IX cerebellar subregions link with the default mode network in our species (Buckner et al., 2011; Diedrichsen et al., 2009; Habas et al., 2009; Halko et al., 2014; Chen & Zhao, 2019). Habas (2009) and Krienen and Buckner (2009) have also shown the associations within

Lobule IX and Crus I. In studies focusing on social cognitive tasks, there was increased activity in the mPFC, precuneus, bilateral TPJ, and cerebellum (Van Overwalle & Mariën, 2016). The involvement of the Crus II in mentalizing was shown in a study conducted by Van Overwalle et al. (2020). DMN overlaps with the social mentalizing network (Mars et al., 2012; Schilbach et al., 2012; Spreng, Mar, & Kim, 2009; Van Overwalle et al., 2015), therefore Barrett and Satpute (2013) proposed the term “default/mentalizing” network, suggesting its function is to create mental models based on past experiences (p. 365, as cited in Van Overwalle et al., 2015). It is hypothesized that the cerebellum’s default network, as identified by Van Overwalle et al. (2014), plays a key role in social mentalizing rather than just supporting executive functions, aligning with Buckner et al. (2011). The posterior cerebellum's "default/mentalizing" network is activated during mentalizing tasks (Van Overwalle et al., 2020).

With studies focusing on the involvement of the cerebellum in mentalization, our understanding of this subject is expanding. A recent study by Metoki et al. (2022) showed the association and link within the left cerebellum and the mentalizing areas in the brain. The findings showed increased connectivity, especially in the left cerebellum. A significant point was the connections between the left cerebellum and the right cerebral mentalizing areas. The anterior temporal lobe (ATL), however, showed this form of lateralization with two cerebellar regions. Their study also demonstrated the presence of loops between the cerebellar and cerebral mentalizing areas, highlighting the involvement of the dMPFC and vMPFC in these circuits (Metoki et al., 2022). A recent meta-analytic connectivity analysis comprising 34 studies and 578 participants supported this conclusion by demonstrating distinct cerebro-cerebellar connections between the mentalizing networks of the cerebellum and cerebrum (Van Overwalle et al., 2015; Overwalle & Steen, 2019). Significantly, the "default/mentalizing" network situated in the posterior cerebellum is engaged in mentalizing tasks (Van Overwalle et al., 2020). Social mentalizing, also known as theory of mind, involves the cognitive processes by which individuals interpret and infer the mental states of others, including their intentions, beliefs, and emotions. The posterior cerebellum, especially Crus II, is exceptionally involved in social cognition. The cerebellar regions involved in social mentalizing are also engaged in sequencing social events and retaining these events' chronological order. This maintenance of sequencing is essential for acknowledging and predicting social interactions (Van Overwalle, Manto, & Cattaneo et al., 2020). The cerebellum has many roles beyond motor control, and its role in complex social cognition and the sequencing of social events is highlighted by the critical role it plays in processing and integrating detailed social information.

To comprehend others' actions and predict their future behaviors, it is crucial to contextualize social mentalizing within the framework of past and future actions. The important part here is the action sequences because an action is considered to be aggressive or defensive depending on the previous sequence. Thus, to read people's minds and form social judgments, one must follow the right behavioral sequence, which is involved in a variety of motor, cognitive, and social skills and makes one’s social interaction more effective (Van Overwalle, Pu, Ma, et al., 2022).

3.5.2 The Cerebellum Sequence Hypothesis: Predictive Modeling in Social Cognition

The human brain is remarkable for its ability to anticipate and prepare for future events, a concept aptly summarized by the phrase "looking into the future." The brain continuously makes predictions about forthcoming events and adjusts these predictions to correct any errors. A prediction involves forming a representation of an expected future event, which influences anticipation. LaBerge (1995) defines anticipation as the phenomenon where heightened neural processing occurs in sensory or motor areas prior to the actual occurrence of a perceptual or motor event (as cited in Bubic, Cramon, & Schubotz, 2010). The cerebellum is considered central to this predictive capability, as it is believed to generate internal models that aid in forecasting future events (Tesche & Karhu, 2000). According to Leggio and Molinari (2014), the cerebellum excels in detecting and simulating repetitive patterns in temporally or spatially structured events. It creates internal models that facilitate predictive functions, enabling the brain to reconstruct sequences of events accurately after detecting violations and recognizing events as part of a series. This brain region helps us predict how others will act and plan our responses accordingly. By simulating social scenarios, the posterior cerebellum improves our ability to anticipate others' behaviors and react effectively (Van Overwalle, Pu, Ma, et al., 2022).

Specifically, the function of the cerebellum is encoding social action sequences that are either rewarding or punitive and commonly experienced in interactions with others (De Zeeuw, Lisberger, & Raymond, 2020; Van Overwalle et al., 2022). This predictive talent, based on prior experiences, enables people to act more successfully. For example, if someone learns that giving positive comments makes people feel better about themselves and others, they will likely start doing so more frequently and unconsciously. People may become more efficient in their social interactions if they discover that providing positive feedback effectively placates others. This might happen gradually and unconsciously (Leggio et al., 2011; Van Overwalle et al., 2022). In an fMRI study, Heleven, van Dun, and Van Overwalle (2019) examined the hypothesis that the cerebellum plays a role in developing social action sequences that reflect or rely on an individual's mental state. The posterior cerebellum was indeed involved in comprehending the correct order of action sequences related to social understanding.

3.6 From Stone Tools to Social Learning: The Cerebellum’s Role in Human Cognition Evolution

Recently, with the cerebellum’s role in social cognition being increasingly recognized, the research has begun to gain notable attention in the field of cerebellar role in human evolutionary neuroscience. Especially Larry Vandervert’s (2016) arguments opened a new area for exploring the cerebellum’s role in humans. He addresses the cerebellar roles in relation to social interaction, communication and cultural learning, which leads him to argue that the cerebellum has a pivotal role in the evolution of Homo sapiens. He argues that the cerebellum has a crucial role in our unconscious learning and the development of human culture, which includes social cognition and language, the key components of human culture evolution. According to Vandervert (2016), through repetitive learning, the cerebellum creates an internal model that can predict and refine the complex behaviors. This, finally leads us to have a cumulative culture, because we as humans share our skills with our species.

In 2017, Stout and Hecht discussed that the development of our cumulative culture was due to our constant improvement of sophisticated mechanisms for learning complex skills through observation and imitation. They give the example of stone making as a survival skill that helped shape our evolution. Stone making requires a variety of abilities such as motor control, planning and problem solving. According to Stout and Hecht (2017), these abilities result in social learning, since we observe, repetitively imitate and practice these skills. In 2018, Smaers et al. conducted a research where they sought to investigate if these complex behaviors in mammals, such as learning and problem solving were in relation to the modifications in the lateral cerebellum, since it is engaged in motor control and cognitive functions. What they explored was that the lateral cerebellum increased in size as the cognitive abilities in primates were better. This finding implies that independent alterations in the lateral cerebellum may have had a parietal role in the evolution of complex behaviors in a variety of mammals. Let's imagine a scenario in which we are making a stone. Vandervert (2018) emphasizes the crucial role of the cerebellum in predicting the breaking point during this stone-making process. He further argues another prediction point of cerebellum and it is the evolution of language which again involves sequences. The cerebellum would be engaged in the prediction and the refinement of these sequences. His discussion is, the cerebellum's influence on both motor skills and cognitive abilities would have made it a key player in the development of human society. Our ability to learn from our observations, in other words, social learning is also deeply rooted in the cerebellum's functions. His research suggests that what makes humans unique may not just be about our cerebral cortex but also about the cerebellum, which helps us socially learn and create the diverse cultures we see today.

(Guevara et al., 2021) compared the lateral cerebellum and dorsolateral prefrontal cortex of the humans, chimpanzees, and rhesus macaques in a genome-wide epigenetic analysis study in order to explore and identify the human-specific epigenetic modifications that differentiate these brain regions. They showed that the human cerebellum exhibits greater differential CpG methylation, an epigenetic marker linked to gene expression, compared to the prefrontal cortex. They address this finding as associated with critical cognitive functions such as language, motor control, and executive processes. They suggest that the cerebellar expression in humans played a key role in the evolution of human-specific cognitive abilities and behaviors, in other words in the human brain evolution. Vandervert, Manto, Adamaszek, Ferrari, Ciricugno & Cattaneo together published a paper in 2024 which further emphasized the cerebellar role in the evolution of our species, by maximizing the social cognitive functions. The cerebellar ability of learning and refining movements and social cognition through repeated practice led us to our cumulative culture, ultimately playing a role in the great evolution of our species.

3.7 Recent Evidence of the Cerebellum's Essential Role in Mentalizing

An increased amount of research has established the cerebellum as a key component of the mentalizing network, with the posterior regions, particularly Crus I and Crus II, playing a significant role in theory of mind tasks. Gathering recent data on the cerebellum's involvement in social cognition is essential to further understand its contribution to these complex processes. Heleven et al. (2019) initially demonstrated the activation of cerebellar Crus areas in the tasks that require mentalizing in social action sequences, compared to the tasks that had non-social sequences using fMRI and Heleven et al. (2021) initially showed that cerebellar TMS had an effect only with social action sequences tasks that required social mentalizing and the posterior cerebellar Crus I & II were activated during implicit learning and predicting new belief sequence tasks. An important question here to consider is if the posterior cerebellum is supporting mentalizing with uniquely specialized certain areas or is it just one of many functions sub-served by the cerebellum. Overwalle et al. (2020) addressed the question in their meta-analysis with a different approach, diverging from the strategies typically employed in other meta-analyses. To understand the role of the cerebellum better, they gathered data from over 200 studies and focused on the specific cerebellar areas first and then examined all studies that showed activation in these regions, instead of identifying the areas that are being activated in the social studies. Since the previous studies showed the significance of the cerebellum in social cognition but did not provide in which way this function was tied to the cerebellum nor did not investigate which mentalizing processes in particular are supported by the cerebellum, they sought to clarify the cerebellum's specific role in social cognition. Their study revealed that social mentalizing and emotional self-experiences are domain specific areas in which the posterior Crus II cerebellum is highly specialized. In this location, these mechanisms were shown in about 74% of the research. However, Crus I exhibited less specialization for mentalizing with a rate of 35%. Crus II showed more involvement in the tasks related to mentalizing and emotional self-experiences and Crus I showed a more diverse task range by being involved in non-mentalizing processes, including cognitive and semantic tasks. Their study has a significant importance for the understanding of the cerebellum in social and emotional cognition and the domain domain-specific specialization. A similar research was done by Metoki et al. in 2021. Their large scale study revealed that the cerebellum had a domain specific organization and there was a significant left cerebellar lateralization in the connections with the cerebral mentalizing areas through cerebello-thalamo-cortical (CTC) and cortico-ponto-cerebellar (CPC) pathways. They underlined the significance of the Crus II in processing social cognitive tasks. The role of the posterior cerebellar Crus II in mentalizing is also shown by Cattaneo et al. (2022). They also investigated its ability to use contextual information to predict actions. Their study demonstrated that Crus II is a specialized area for social mentalizing and emotional self-experiences, showing distinct connectivity with social networks in the cerebral cortex. The medial-to-lateral gradient task engagement in the posterior cerebellum was shown by Ferrari et al. in 2023. While the middle part of the cerebellum is engaged in emotion recognition, the lateral parts were more involved in tasks requiring higher-level processing and mentalizing. Catoira et al. (2023) used both transcranial direct current stimulation (tDCS) and magnetic resonance imaging (MRI) to assess the cerebellar roles in mentalizing in 23 participants. They started with applying tDCS while the participants were in the MRI scanner and following the tDCS they immediately measured their brain activity. The task included requirements for generating correct sequences of social actions involving false and true beliefs, social routines and non-social (control) events. Their findings demonstrated that stimulation decreased task performance as well as brain activation in important mentalizing regions such as precuneus, temporo-parietal junction and the cerebellum, showing the significance of the cerebellum in mentalizing network and its function in social sequence processing. While the non-invasive brain stimulation methods shed light on the cerebellum's role in cognitive functions, Pezzetta et al. (2024) investigated their effect on cerebellum-related cognitive processes by reviewing 66 studies. What they found was that cognitive performance got better with tDCS on the medial cerebellum, however it got disrupted by TMS, especially when it was over lateral cerebellum. The negative effects were also seen when they applied low-frequency TMS and constant theta burst stimulation (cTBS). Their study compared the effect of the stimulation methods and provided insight for further research.

In 2024, Vandervert et al. conducted an interesting study where they investigated the cerebellar role in the evolution of our species, by maximizing the social cognitive functions. According to their study, our repetitive activities, like stone-tool making, which to Stout and Hecht (2017) was the beginning of our cumulative culture (as cited in Vandervert et al, 2024) were possible thanks to the cerebellar ability of learning and refining movements and social cognition through repeated practice where it led us to our cumulative culture.

Cerebral Cortex Initiates **Repetition** of
Movement, Thought, Social Interaction
↓
Internal Models Learned in Cerebellum **Predict Sequences**
of Movement, Thought, Social Interaction
↓
Enlargement of Cerebellar Cortices
↓
Continued Repetition **Optimizes** Cerebellar Internal Models in
a **Positive Feedback Loop** Toward Goal-Related Movement, Thought,
Social Interaction Initiated in Cerebral Cortex
↓
CUMULATIVE CULTURE
(Progressively Advanced Tools, Novel Movement, Thought, Social Interaction)

Figure 5: Repetition of movement, thought, and social interaction initiated in the cerebral cortex leads to optimization of goals via internal models learned in the cerebellum. This creates a positive feedback loop leading to advances in cumulative culture (Vandervert et al., 2024).

Since our cumulative culture has our language and art in it, the rise of our complex behaviors and the emergence of modern humans were aided by the cerebellum and the cerebrum. Hence, the cerebellum played a pivotal role in our species' triumph, enhancing our cognitive abilities, improving our social interactions, and perfecting our tool-making skills, ultimately guiding us towards greatness, *and the rise of Homo sapiens* (Vandervert et al, 2024).

4. EXPERIMENTAL SECTION: PROTOCOL DESIGN

We aimed to investigate the cerebellum’s role in mentalizing through transcranial magnetic stimulation (TMS). Our participants engaged in the Yoni task by Shamay-Tsoory & Aharon-Peretz (2007), designed to assess cognitive, affective, and physical state attributions. The study aims to determine whether TMS applied to the cerebellum affects participants' response times and accuracy during mentalizing tasks (i.e., understanding others' mental states). In light of previous neuroimaging studies, We hypothesized that the cerebellumplays a significant role in higher cognitive processes, including mentalizing.

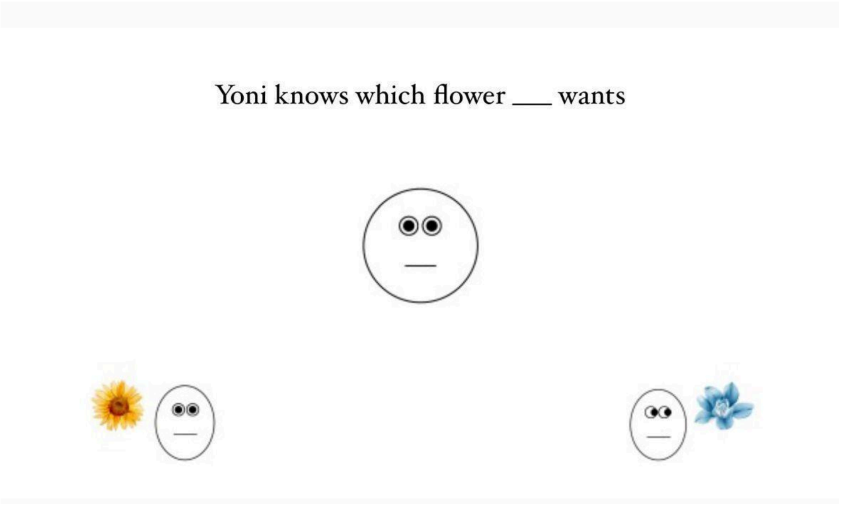
4.1 Materials and Methods

16 Italian volunteers (6 males, 8 females mean age= 24.5 years, SD= 3.16). participated in the experiment. All participants were right-handed, as assessed using the Edinburgh Handedness Questionnaire (Oldfield, 1971). All participants had normal or corrected-to-normal vision. Before the TMS experiment, written informed consent was obtained from the participants, who filled in a questionnaire to evaluate compatibility with TMS (Rossi et al., 2011). None of them had a history of epilepsy, brain trauma, or neurological disorders. The local ethical committee approved the protocol and participants were treated in accordance with the Declaration of Helsinki.

Participants performed a modified version of the Yoni task. Task (Shamay-Tsoory & Aharon-Peretz, 2007), a computerized task designed to evaluate the ability to judge affective and cognitive mental state attributions using simple verbal instructions and visual contextual cues involving minimal executive demands (Shamay-Tsoory & Aharon-Peretz, 2007). The Yoni task has been widely used in patients, neuroimaging, and neurostimulation studies (Kalbe et al., 2010; Bodden et al., 2013; Holbrook et al., 2021; Rossetto et al., 2018; Shamay-Tsoory & Aharon-Peretz, 2007; Shamay-Tsoory et al., 2007). The Yoni task is organized into three sub-tasks: the Yoni affective task, the Yoni cognitive task, and the Yoni physical task.

The Yoni cognitive task consists of 35 trials, each showing a cartoon face (named *Yoni*) in the center of the screen and two black and white pictures below, one in each corner of the screen. The task was designed to assess second-order cognitive mentalizing. Participants had to infer Yoni's mental state in relation to another character's mental state. Specifically, in each trial, the participants must choose the correct image to which Yoni is referring based on an incomplete sentence on the top of the screen and *Yoni*'s facial expression. Some examples of sentences are "Yoni knows which flower ___ wants." The correct answer can be selected only by reasoning about Yoni's mental state by referring to other characters' affective mental states. The cognitive Yoni task included verbs: think_want, want_think, think_ do not want, think_think, know_want, want_ignore, do not think_do not want. Examples are provided below:

Yoni knows which flower ___ wants. (Right)
Yoni thinks about the fruit that ___ thinks about. (Right)
Yoni wants the animal that ___ thinks about. (Left)

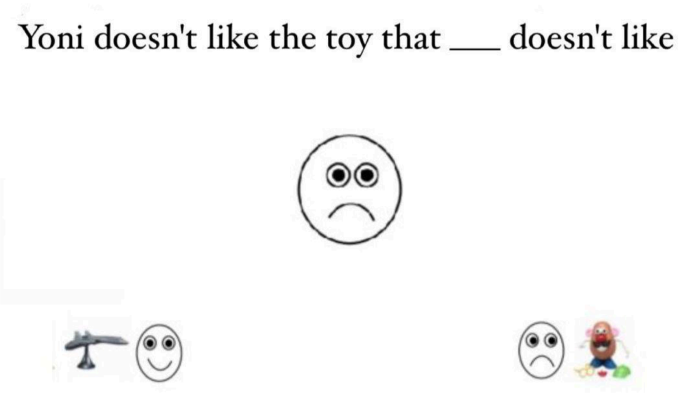


Yoni knows which flower ___ wants

The affective Yoni task was identical to the cognitive Yoni task with the exception that it included verbs like envy, gloat, identify, like_like, like_dislike, dislike_like, dislike_dislike, that refer to emotional (vs. cognitive) states. Examples are provided below:

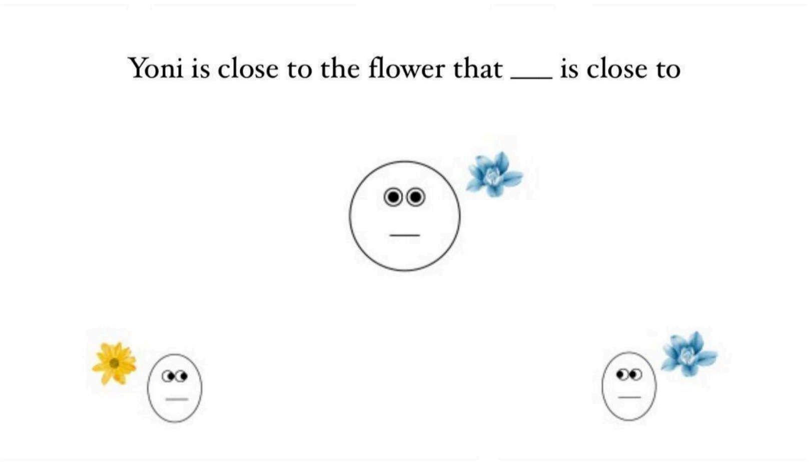
Yoni doesn't like the toy that ___ doesn't like. (Right)
Yoni envies the success of ___. (Right)

Yoni gloated over the misfortune of ___. (Right)



Finally, the **Yoni physical task** is identical to the Yoni cognitive task except its focus on physical states and actions rather than mental states. Specifically, the physical task does not involve any references to mentalizing, emotions, or social inferences and instead uses verb pairs that describe physical states or actions, such as proximity or possession. The Physical tasks included words/word pairs: have_do not have, be close_ be close, have_be close, be close_ have, own_ be close, be close_own, missing_have. Examples are provided below:

Yoni is close to the flower that ___ is close to. (Right)
Yoni is close to the toy that ___ has. (Left)
Yoni has the animal that ___ is close to. (Left)



For each task, each trial started with a black fixation cross (2500 ms), and then the sentence and Yoni’s face appeared on the screen. After reading the sentence and observing Yoni’s face, participants pressed the spacebar to make the two response options appear. Participants responded as quickly as possible by using their left hand to press the left or right arrow key corresponding to the position of the image on the screen. The location (right/left corner) of the correct response was counterbalanced.

Participants sit in front of a 19’ screen at an approximate distance of 60 cm. After a practice block, participants performed the three yoni tasks (one for each TMS condition, see below) (the order of the task performance was counterbalanced for each participant). For stimulus presentation, data collection, and TMS triggering, the software E-prime 2.0 (Psychology Software Tools, Pittsburgh, PA) was used.

4.1.1 TMS

TMS was delivered using a Magstim Rapid^2 stimulator (Magstim Co., Ltd, Whitland, UK) connected to a 70-mm figure of eight coil. At the beginning of the session, the individual motor threshold (MT) for each participant was determined by applying single-pulse TMS over the left primary motor cortex (M1). The motor threshold was defined as the minimum level of intensity at which there is a 50% probability of producing motor evoked potentials (MEP) $\geq$ 50 µv peak to peak in subjects at rest, that is in 5 out of 10 consecutive trials (Hanajima et al., 2007; Rossini et al., 1994). During each session, stimulation intensity was set at 100% of each participant's individual MT. Triple-pulse TMS was delivered 150 ms after the presentation of the response options with a frequency of stimulation of 20 Hz. This frequency of cerebellar TMS has been previously found effective in modulating behavioral responses (Cattaneo et al., 2014; Ferrari et al., 2018; Koch et al., 2007). The intensity of the stimulation was kept constant during the stimulation of all three target sites, which were the left lateral cerebellum, the right lateral cerebellum, and the vertex (control site). The anatomical Talairach coordinates (Talairach & Tournoux, 1998) of the left lateral cerebellum were x=-31, y=-64, z=-27, and Talairach coordinates of the right lateral cerebellum were x=30, y=-60, z=-30 (the coordinates correspond to cerebellar activations during emotional processing, see Keren-Happuch et al., 2014). The sites of stimulation were identified using a stereotaxic neuronavigation system, which allows recreating estimated magnetic resonance images (MRI) for each subject through a 3D warping procedure fitting a high-resolution MRI template with the participants' scalps models and craniometric points (Softaxic 2.0, EMS, Bologna, Italy). This procedure was previously used in several studies (Cattaneo et al., 2015; Ferrari et al., 2016; Ferrari et al., 2018a). The coil was positioned tangentially to the scalp and parallel to the midsagittal line, with the handle pointing superiorly for the stimulation of the cerebellum and pointing backward for the stimulation of the vertex. The order of the stimulation sites was counterbalanced for each participant.

5. RESULTS

Mean accuracy rates and mean reaction times (RTs) were computed for each participant in each experimental condition. Two participants were identified as outliers and excluded from the final analysis to ensure the integrity and accuracy of the results. Accuracy scores and RT for correct responses were analyzed using separate repeated-measures ANOVAs with Task (affective, cognitive vs. physical), and TMS (left cerebellum, right cerebellum, and vertex) as within-subjects variables.

The ANOVA on mean accuracy scores revealed nonsignificant main effects of Task, $F(2, 26) = 0.89$, $p = .423$, or TMS, $F(2, 26) = .29$, $p = .748$. The interaction between Task and TMS was not significant, $F(4,52)=2.20$, $p=.082$.

The ANOVA on reaction times revealed a **significant** main effect of Task, $F(2,26)=7.347$, $p=.003$, indicating that the cognitive task required longer reaction times than the other tasks. The main effect of TMS, $F(4,52)<1$, $p = .73$, and the interaction Task by TMS $F(2,26)=<1$, $p=0.413$, were not significant.

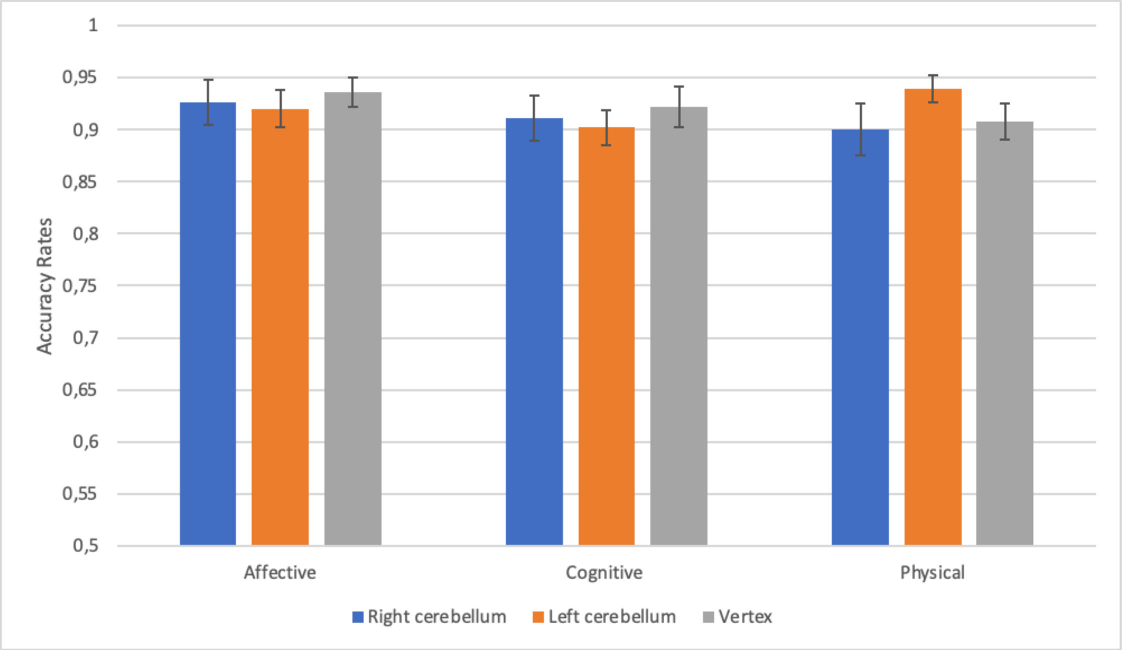


Figure 1: Accuracy rates with standard error for the affective, cognitive, and physical tasks.

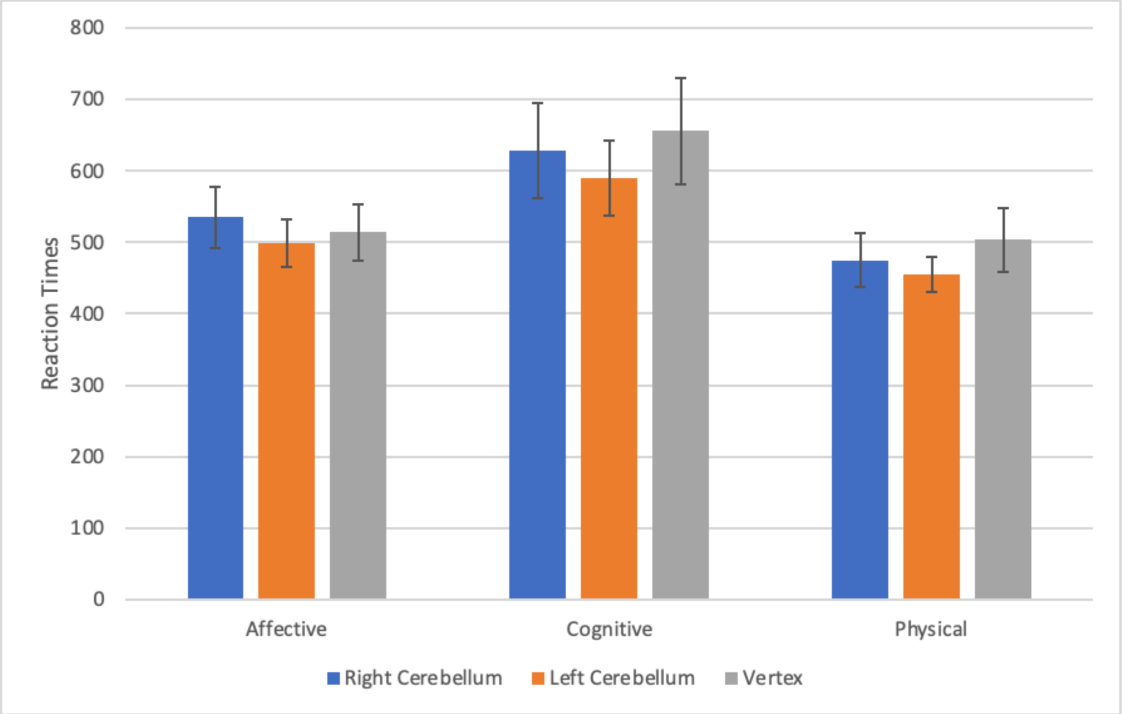


Figure 2: Reaction times with standard error for the affective, cognitive, and physical tasks.

5.1 DISCUSSION

The aim of our study was to investigate the cerebellum's role in mentalizing by using transcranial magnetic stimulation (TMS). Historically, the cerebellum has been primarily recognized for its role in motor control and coordination (Flourens, 1824; Ito, 1984; Glickstein et al., 2009; Marr, 1969; Albus, 1971). However, recent research has increasingly suggested that the cerebellum is involved in functions beyond motor control (Rawson, 1932). A substantial body of evidence now indicates that the cerebellum also plays a critical role in cognitive processes (Schmahmann & Sherman, 1998; Guell, Hoche, & Schmahmann, 2015). Recent research also suggests the crucial involvement of the cerebellum in the limbic system (Adamaszek et al., 2017; Schmahmann, 2019) and that it is engaged in emotion processing (Fusar-Poli et al., 2009; Adamaszek et al., 2014; Hoche et al., 2016; Clausi et al., 2021). Lately, cerebellar research has shown the essential role of the cerebellum in social cognition and its being a part of the social brain (Van Overwalle et al., 2014, 2019, 2020; Stoodley & Schmahmann, 2010). In our study, we wanted to further investigate the cerebellar roles in mentalizing, which have been shown by a wide range of research (Schmahmann & Sherman, 1998; Adamaszek et al., 2014; Van Overwalle et al., 2014, 2020; Clausi et al., 2021; Ferrari et al., 2023).

To further explore the involvement of the cerebellum in mentalizing, we sought to modify the cerebellar activity as participants performed the Yoni task (Shamay-Tsoory and Aharon-Peretz, 2007) which aims to distinguish the affective and cognitive aspects of theory of mind. In our study, our participants had to answer the questions of the cognitive Yoni task, the affective Yoni task, and the physical Yoni task. We applied TMS to the left cerebellum, the right cerebellum and the vertex as the control site and used ANOVA to analyze our data and to examine the accuracy and the reaction times of our participants. From the visual exploration of the data, we can observe that the cerebellar stimulation tended to affect the three tasks to a different extent. In the Yoni Affective and Yoni cognitive tasks, we can appreciate a small decrement in performance during TMS of both cerebellar sites (vs. Vertex), possibly stronger in the left cerebellar hemisphere. In the Yoni physical tasks, in turn, cerebellar TMS seems to have a different effect on performance, with an increment in accuracy rates during TMS over the left cerebellum.

The tendency we observed in accuracy may point to the cerebellum's potential role in modulating cognitive performance in specific contexts. Previous research has demonstrated that the cerebellum contributes significantly to higher cognitive processes (Stoodley & Schmahmann, 2018), affective regulation (Schmahmann & Sherman, 1998), and theory of mind (Van Overwalle et al., 2014). The identification of Cerebellar Cognitive Affective Syndrome (CCAS) has further highlighted the cerebellum's involvement in cognitive functioning, revealing changes in executive functions (Schmahmann & Sherman, 1998). Van Overwalle et al. (2014) also showed that cerebellar regions overlap with areas engaged in sensorimotor and executive functioning. In this context, the cerebellum may facilitate the refinement of cognitive processes, particularly in tasks that require error correction, prediction, and adaptation. The interaction between TMS and task accuracy observed in our study may reflect the cerebellum’s role in dynamically modulating cognitive resources, particularly in tasks that demand both cognitive and affective mentalizing. The increment in accuracy rates we observed during TMS over the left cerebellum aligns with findings from several previous studies. Metoki et al. (2022) demonstrated a significant association between the left cerebellum and mentalizing regions in the brain. Their study revealed increased connectivity, particularly involving the left cerebellum, further highlighting its role in social cognition processes. Also Ferrari et al. (2023) showed that the lateral parts of the cerebellum were more involved in tasks requiring higher-level processing and mentalizing. Pezzetta et al. (2024) found that cognitive performance got better with tDCS on the medial cerebellum, however it got disrupted by TMS, especially when it was over lateral cerebellum.

We also observed that participants took more to perform the cognitive compared to the affective or physical tasks. Our observation aligns with previous research, such as Shamay-Tsoory & Aharon-Peretz (2007), which found that participants took longer to complete cognitive theory of mind (ToM) tasks compared to affective and physical tasks. They suggested that cognitive ToM involves more complex processing, contributing to longer response times. Similarly, Kalbe et al. (2010) observed faster reaction times for affective ToM tasks, indicating these tasks may rely on different or less demanding processing mechanisms. In a more recent study, Allain et al. (2024) found that Huntington's Disease (HD) patients exhibited greater impairments in cognitive ToM compared to affective ToM, particularly in complex tasks, with stage II patients showing significant delays in cognitive ToM performance. These findings support the notion that cognitive ToM tasks require more processing, which explains the longer response times observed in our study.

Our results are partially in line with our hypothesis regarding cerebellar roles in mentalizing and they align with the previous experiments showing the cerebellar involvement in mentalizing (Buckner *et al.*, 2011; Van Overwalle et al., 2014; Van Overwalle et al. 2015a.; Heleven et al., 2019; Van Overwalle et al.,2020; Heleven et al., 2021; Metoki et al., 2022; Cattaneo et al., 2022; Catoira et al., 2023). Our research highlights the cerebellum's possible role in modulating performance in complex tasks, which could inform future studies and improve our understanding of the neural mechanisms underlying social cognition and mentalizing. We suggest that while TMS's impact on accuracy isn't immediately obvious, there's potential for significant effects that could be revealed in future experiments with refined techniques or larger datasets. Considering the impact of social cognition in disorders and the importance of mentalizing in human interactions, investigating the role of the cerebellum in social cognition holds an important area which can be beneficial for those who suffer from social cognitive impairments by suggesting new areas to improve.

5.2 LIMITATIONS

While our study sheds light on the cerebellum's function in mentalizing, it is crucial to be aware of the limitations that could affect the interpretation and generalizability of the results. By pointing out these limitations, our results can be interpreted more carefully and highlight the areas that should be paid attention to for future research.

Firstly, one of the primary limitations of our study is our sample size. Our final data only consists of 14 participants which is a small sample size. The small number of the participants may not represent the broader population, affecting the generalizability of the results. With a small sample size, the observed effects could be due to the variables and individual differences such as their cognitive abilities or previous experiences. In addition, our small sample size reduces the statistical power of our study. This might be one of the reasons why our observed effect size is not statistically significant, which can lead to false negatives.

Secondly, while we are investigating the cerebellar roles in mentalizing, we used a single task paradigm. Our study focused on Yoni tasks only, even though it had three components assessing different aspects of mentalizing. Relying only on Yoni tasks might not capture the complex roles of the cerebellum in social cognition, especially in mentalizing. By relying solely on the Yoni task, we may have overlooked other crucial aspects of mentalizing, such as empathy or sarcasm, where the cerebellum could play a significant role. Yet, our study was limited to this single experimental framework.

Our third limitation is our participant profile. In our study, our participants were exclusively Italian university students, where the average level of understanding and cognitive ability was relatively consistent. To represent a broader population, we could have included additional demographic factors, such as different age groups, work backgrounds, ethnicity or social interaction in day-to-day living. However, due to our lack of diversity, the generalizability of our findings is limited.

Another potential limitation can be the length and the structure of our study. Our study lasted approximately two hours. During these two hours, our participants underwent stimulation on the left cerebellum, right cerebellum, and vertex separately, for the affective, cognitive, and physical Yoni tasks. This length and the multiple stimulation sessions may have been tiring for the participants, potentially impacting their performance and the reliability of the results over time.

5.3 CONCLUSION

Our study provides significant insights into the cerebellum's involvement in mentalizing. By using transcranial magnetic stimulation (TMS) during the Yoni task, we have demonstrated the cerebellum's contribution beyond its traditionally understood motor functions, underscoring its importance in higher cognitive processes. Our findings indicate that cerebellar stimulation impacts both response times and accuracy in cognitive mentalizing tasks, reinforcing the cerebellum's role in complex social interactions. We found that stimulating the cerebellum with TMS affected task accuracy differently across the tasks. Specifically, in the Yoni Affective and Cognitive tasks, our study revealed a slight decrease in performance during cerebellar stimulation, especially in the left hemisphere. In contrast, in the Yoni Physical task, TMS over the left cerebellum resulted in an improvement in accuracy. These findings suggest that the cerebellum's involvement in mentalizing may vary depending on the specific cognitive demands of the task. The tendencies we observed in accuracy support the notion that the cerebellum plays a role in modulating cognitive performance in particular contexts. Our study contributes to the existing body of research by indicating that the cerebellum plays a dynamic role in regulating cognitive resources, particularly in tasks that engage both cognitive and affective mentalizing processes. Advancing our understanding of the cerebellum's role in mentalizing, along with the most effective applications of TMS, opens new possibilities for therapeutic interventions, particularly for individuals with neuropsychiatric disorders such as autism and schizophrenia, where mentalizing deficits are prevalent. Future research should explore how modulating brain networks could improve social cognitive function in clinical populations. In summary, studying the cerebellum’s role in mentalizing enhances our understanding of human cognition and holds promise for improving life quality for those with social cognitive impairments.

6. BIBLIOGRAPHY

Abell, F., Happé, F., & Frith, U. (2000). Do triangles play tricks? Attribution of mental states to animated shapes in normal and abnormal development. *Cognitive Development, 15*(1), 1-16. https://doi.org/10.1016/S0885-2014(00)00014-9

Ackermann, H., & Ziegler, W. (1991). Articulatory deficits in parkinsonian dysarthria: An acoustic analysis. *Journal of Neurology, Neurosurgery & Psychiatry, 54*(12), 1093–1098. https://doi.org/10.1136/jnnp.54.12.1093

Adamaszek, M., D'Agata, F., Ferrucci, R., Habas, C., Keulen, S., Kirkby, K. C., Leggio, M., Mariën, P., Molinari, M., Moulton, E., Orsi, L., Van Overwalle, F., Papadelis, C., Priori, A., Sacchetti, B., Schutter, D. J., Styliadis, C., & Verhoeven, J. (2017). Consensus paper: Cerebellum and emotion. *Cerebellum, 16*(2), 552-576. https://doi.org/10.1007/s12311-016-0815-8

Adolphs, R. (2001). The neurobiology of social cognition. *Current Opinion in Neurobiology, 11*(2), 231-239. https://doi.org/10.1016/s0959-4388(00)00202-6

Adolphs, R. (2010). What does the amygdala contribute to social cognition? *Annals of the New York Academy of Sciences, 1191*(1), 42-61. https://doi.org/10.1111/j.1749-6632.2010.05445.x

Akakin, A., Peris-Celda, M., Kilic, T., Seker, A., Gutierrez-Martin, A., & Rhoton, A. Jr. (2014). The dentate nucleus and its projection system in the human cerebellum: The dentate nucleus microsurgical anatomical study. *Neurosurgery, 74*(4), 401–424; discussion 424–425. https://doi.org/10.1227/NEU.0000000000000293

Albright, T. D., Jessell, T. M., Kandel, E. R., & Posner, M. I. (2001). Progress in the neural sciences in the century after Cajal (and the mysteries that remain). *Annals of the New York Academy of Sciences, 929*(1), 11-40. https://doi.org/10.1111/j.1749-6632.2001.tb05704.x

Albus, J. S. (1971). A theory of cerebellar function. *Mathematical Biosciences, 10*(1–2), 25-61. https://doi.org/10.1016/0025-5564(71)90051-4

Allain, P., Caillaud, M., Prundean, A., Scherer-Gagou, C., & Verny, C. (2024). Affective and cognitive components of theory of mind in Huntington's Disease: Yoni task performance in early and mid-disease stages. *Journal of Neurology, Neurosurgery & Psychiatry*, 95(Suppl 1): A1–A193.

American Psychiatric Association (1980) Diagnostic and statistical manual of mental disorders. 3rd ed. American Psychiatric Association, Arlington, VA.

Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: The medial frontal cortex and social cognition. *Nature Reviews Neuroscience, 7*(4), 268-277. https://doi.org/10.1038/nrn1884

Andreasen, N. C., & Pierson, R. (2008). The role of the cerebellum in schizophrenia. *Biological Psychiatry, 64*(2), 81-88. https://doi.org/10.1016/j.biopsych.2008.01.003

Apps, M. A., Rushworth, M. F., & Chang, S. W. (2016). The anterior cingulate gyrus and social cognition: Tracking the motivation of others. *Neuron, 90*(4), 692-707. https://doi.org/10.1016/j.neuron.2016.04.018

Arioli, M., Cattaneo, Z., Ricciardi, E., & Canessa, N. (2021). Overlapping and specific neural correlates for empathizing, affective mentalizing, and cognitive mentalizing: A coordinate-based meta-analytic study. *Human Brain Mapping, 42*(14), 4777-4804. https://doi.org/10.1002/hbm.25570

Awh, E., Jonides, J., Smith, E. E., Schumacher, E. H., Koeppe, R. A., & Katz, S. (1996). Dissociation of storage and rehearsal in verbal working memory: Evidence from PET. *Psychological Science, 7*(1), 25–31.

Azevedo, F. A. C., Carvalho, L. R. B., Grinberg, L. T., Farfel, J. M., Ferretti, R. E. L., Leite, R. E. P., Filho, W. J., Lent, R., & Herculano-Houzel, S. (2009). *Equal numbers of neuronal and nonneuronal cells make the human brain an isometrically scaled-up primate brain*. Journal of Comparative Neurology, 513, 532–541. https://doi.org/10.1002/cne.21974

Baez, S., Marengo, J., Perez, A., Huepe, D., Font, F. G., Rial, V., Gonzalez-Gadea, M. L., Manes, F., & Ibanez, A. (2015). Theory of mind and its relationship with executive functions and emotion recognition in borderline personality disorder. *Journal of Neuropsychology, 9*(2), 203-218. https://doi.org/10.1111/jnp.12046

Balsters, J. H., Cussans, E., Diedrichsen, J., Phillips, K. A., Preuss, T. M., Rilling, J. K., & Ramnani, N. (2010). Evolution of the cerebellar cortex: The selective expansion of prefrontal-projecting cerebellar lobules. *NeuroImage, 49*(3), 2045-2052. https://doi.org/10.1016/j.neuroimage.2009.10.045

Baron-Cohen, S., & Wheelwright, S. (2004). The empathy quotient: An investigation of adults with Asperger syndrome or high functioning autism, and normal sex differences. *Journal of Autism and Developmental Disorders, 34*(2), 163-175. https://doi.org/10.1023/B:JADD.0000022607.19833.00

Baron-Cohen, S., Leslie, A. M., & Frith, U. (1985). Does the autistic child have a "theory of mind"? *Cognition, 21*(1), 37-46. https://doi.org/10.1016/0010-0277(85)90022-8

Baron‐Cohen, S., Jolliffe, T., Mortimore, C., & Robertson, M. (1997). Another advanced test of theory of mind: Evidence from very high functioning adults with autism or Asperger syndrome. *Journal of Child psychology and Psychiatry*, *38*(7), 813-822.

Barton, R. A., & Venditti, C. (2014). Rapid evolution of the cerebellum in humans and other great apes. *Current Biology, 24*(20), 2440–2444. https://doi.org/10.1016/j.cub.2014.08.056

Baumann, O., & Mattingley, J. B. (2012). Functional topography of primary emotion processing in the human cerebellum. *NeuroImage, 61*(4), 805–811. https://doi.org/10.1016/j.neuroimage.2012.03.044

Beer, J. S., & Ochsner, K. N. (2006). Social cognition: A multi-level analysis. *Brain Research, 1079*(1), 98–105. https://doi.org/10.1016/j.brainres.2006.01.002

Beuriat, P. A., Cohen-Zimerman, S., Smith, G. N. L., & et al. (2022). Evidence of the role of the cerebellum in cognitive theory of mind using voxel-based lesion mapping. *Scientific Reports, 12*, 4999. https://doi.org/10.1038/s41598-022-09104-0

Blakemore, S.-J., Bristow, D., Bird, G., Frith, C., & Ward, J. (2005). Somatosensory activations during the observation of touch and a case of vision–touch synaesthesia. *Brain, 128*(7), 1571-1583. https://doi.org/10.1093/brain/awh500

Blakemore, S. J. (2008). The social brain in adolescence. *Nature Reviews Neuroscience, 9*(4), 267-277. https://doi.org/10.1038/nrn2353

Blatt, G. J., Oblak, A. L., & Schmahmann, J. D. (2013). Cerebellar connections with limbic circuits: Anatomy and functional implications. In M. Manto, J. D. Schmahmann, F. Rossi, D. L. Gruol, & N. Koibuchi (Eds.), *Handbook of the cerebellum and cerebellar disorders* (pp. 479–497). Springer. https://doi.org/10.1007/978-94-007-1333-8_22

Bora, E., & Berk, M. (2016). Theory of mind in major depressive disorder: A meta-analysis. *Journal of Affective Disorders, 191*, 49-55. https://doi.org/10.1016/j.jad.2015.11.023

Bora, E., Vahip, S., Gonul, A. S., Akdeniz, F., Alkan, M., Ogut, M., & Eryavuz, A. (2005). Evidence for theory of mind deficits in euthymic patients with bipolar disorder. *Acta Psychiatrica Scandinavica, 112*(2), 110-116. https://doi.org/10.1111/j.1600-0447.2005.00570.x

Boven, E., & Cerminara, N. L. (2023). Cerebellar contributions across behavioural timescales: A review from the perspective of cerebro-cerebellar interactions. *Frontiers in Systems Neuroscience, 17*, Article 1211530. https://doi.org/10.3389/fnsys.2023.1211530

Brothers, L. (1990). The social brain: A project for integrating primate behaviour and neurophysiology in a new domain. *Concepts in Neuroscience, 1*, 27–51.

Brothers, L., Ring, B., & Kling, A. (1990). Response of neurons in the macaque amygdala to complex social stimuli. *Behavioural Brain Research, 41*(3), 199-213. https://doi.org/10.1016/0166-4328(90)90108-Q

Bubic, A., Von Cramon, D. Y., & Schubotz, R. I. (2010). Prediction, cognition and the brain. *Frontiers in human neuroscience*, *4*, 1094.

Buckner, R. L. (2013). The cerebellum and cognitive function: 25 years of insight from anatomy and neuroimaging. *Neuron, 80*(3), 807-815. https://doi.org/10.1016/j.neuron.2013.10.044

Buckner, R. L., Andrews‐Hanna, J. R., & Schacter, D. L. (2008). The brain's default network: anatomy, function, and relevance to disease. *Annals of the new York Academy of Sciences*, *1124*(1), 1-38.

Buckner, R. L., Krienen, F. M., Castellanos, A., Diaz, J. C., & Yeo, B. T. (2011). The organization of the human cerebellum estimated by intrinsic functional connectivity. *Journal of Neurophysiology, 106*(5), 2322-2345. https://doi.org/10.1152/jn.00339.2011

Catoira, B., Van Overwalle, F., Van Schuerbeek, P., Raeymaekers, H., Heleven, E., Baetens, K., Deroost, N., & Baeken, C. (2023). The effects of stimulating the cerebellum on social sequences: A tDCS-fMRI pilot study. *International Journal of Clinical and Health Psychology, 23*(3), 100373. https://doi.org/10.1016/j.ijchp.2023.100373

Cattaneo, Z., Ferrari, C., Ciricugno, A., Heleven, E., Schutter, D. J. L. G., Manto, M., & Van Overwalle, F. (2022). New horizons on non-invasive brain stimulation of the social and affective cerebellum. *Cerebellum, 21*(3), 482-496. https://doi.org/10.1007/s12311-021-01300-4

Cattaneo, Z., Lega, C., Ferrari, C., Vecchi, T., Cela-Conde, C. J., Silvanto, J., & Nadal, M. (2015). The role of the lateral occipital cortex in aesthetic appreciation of representational and abstract paintings: A TMS study. *Brain and Cognition, 95*, 44-53. https://doi.org/10.1016/j.bandc.2015.01.008

Cattaneo, Z., Renzi, C., Casali, S., Silvanto, J., Vecchi, T., Papagno, C., & D'Angelo, E. (2014). Cerebellar vermis plays a causal role in visual motion discrimination. *Cortex, 58*, 272-280. https://doi.org/10.1016/j.cortex.2014.01.012

Chen, G., Zhao, L., Jia, Y., Zhong, S., Chen, F., Luo, X., Qiu, S., Lai, S., Qi, Z., Huang, L., & Wang, Y. (2019). Abnormal cerebellum-DMN regions connectivity in unmedicated bipolar II disorder. *Journal of Affective Disorders, 243*, 441-447. https://doi.org/10.1016/j.jad.2018.09.076

Ciricugno, A., Ferrari, C., Battelli, L., & Cattaneo, Z. (2024). A chronometric study of the posterior cerebellum's function in emotional processing. *Current Biology, 34*(9), 1844–1852.e3. https://doi.org/10.1016/j.cub.2024.03.013

Coco, M., & Perciavalle, V. (2015). Where did the motor function of the cerebellum come from? *Cerebellum & Ataxias, 2*, 10. https://doi.org/10.1186/s40673-015-0029-8

Cusi, A. M., Nazarov, A., Holshausen, K., MacQueen, G. M., & McKinnon, M. C. (2012). Systematic review of the neural basis of social cognition in patients with mood disorders. *Journal of Psychiatry and Neuroscience, 37*(3), 154-169. https://doi.org/10.1503/jpn.100179

Damasio, A. R. (1994). *Descartes' error: Emotion, reason, and the human brain*. New York: Grosset/Putnam.

De Benedictis, A., Rossi-Espagnet, M. C., de Palma, L., Carai, A., & Marras, C. E. (2022). Networking of the human cerebellum: From anatomo-functional development to neurosurgical implications. *Frontiers in Neurology, 13*, Article 806298. https://doi.org/10.3389/fneur.2022.806298

De Vidovich, G. Z., Muffatti, R., Monaco, J., Caramia, N., Broglia, D., Caverzasi, E., Barale, F., & D'Angelo, E. (2016). Repetitive TMS on left cerebellum affects impulsivity in borderline personality disorder: A pilot study. *Frontiers in Human Neuroscience, 10*, 582. https://doi.org/10.3389/fnhum.2016.00582

Dekeyzer, S., Vanden Bossche, S., & De Cocker, L. (2023). Anything but little: A pictorial review on anatomy and pathology of the cerebellum. *Clinical Neuroradiology, 33*(4), 907–929. https://doi.org/10.1007/s00062-023-01326-7

Depping, M. S., Schmitgen, M. M., Kubera, K. M., & Wolf, R. C. (2018). Cerebellar contributions to major depression. *Frontiers in Psychiatry, 9*, 634. https://doi.org/10.3389/fpsyt.2018.00634

Desmond, J. E., & Fiez, J. A. (1998). Neuroimaging studies of the cerebellum: Language, learning, and memory. *Trends in Cognitive Sciences, 2*(9), 355-362. https://doi.org/10.1016/s1364-6613(98)01211-x

Devinsky, O., Morrell, M. J., & Vogt, B. A. (1995). Contributions of anterior cingulate cortex to behaviour. *Brain, 118*(1), 279–306. https://doi.org/10.1093/brain/118.1.279

Dunbar, R. I. M., & Shultz, S. (2007). Evolution in the social brain. *Science, 317*(5843), 1344-1347. https://doi.org/10.1126/science.1145463

Ecker, C., Ronan, L., Feng, Y., & Williams, S. C. (2013). Intrinsic gray-matter connectivity of the brain in adults with autism spectrum disorder. *Proceedings of the National Academy of Sciences, 110*(32), 13222-13227. https://doi.org/10.1073/pnas.1221880110

Ferrari, C., Cattaneo, Z., Oldrati, V., Casiraghi, L., Castelli, F., D'Angelo, E., & Vecchi, T. (2018). TMS over the cerebellum interferes with short-term memory of visual sequences. *Scientific Reports, 8*(1), 6722. https://doi.org/10.1038/s41598-018-25151-y

Ferrari, C., Ciricugno, A., Arioli, M., & Cattaneo, Z. (2023). Functional segregation of the human cerebellum in social cognitive tasks revealed by TMS. *Journal of Neuroscience, 43*(20), 3708-3717. https://doi.org/10.1523/JNEUROSCI.1818-22.2023

Ferrari, C., Ciricugno, A., Urgesi, C., & Cattaneo, Z. (2022). Cerebellar contribution to emotional body language perception: A TMS study. *Social Cognitive and Affective Neuroscience, 17*(1), 81–90. https://doi.org/10.1093/scan/nsz074

Ferrari, C., Fiori, F., Suchan, B., Plow, E. B., & Cattaneo, Z. (2021). TMS over the posterior cerebellum modulates motor cortical excitability in response to facial emotional expressions. *European Journal of Neuroscience, 53*(4), 1029–1039. https://doi.org/10.1111/ejn.14953

Ferrari, C., Oldrati, V., Gallucci, M., Vecchi, T., & Cattaneo, Z. (2018). The role of the cerebellum in explicit and incidental processing of facial emotional expressions: A study with transcranial magnetic stimulation. *NeuroImage, 169*, 256-264. https://doi.org/10.1016/j.neuroimage.2017.12.026

Ferrucci, R., Giannicola, G., Rosa, M., Fumagalli, M., Boggio, P. S., Hallett, M., Zago, S., & Priori, A. (2012). Cerebellum and processing of negative facial emotions: Cerebellar transcranial DC stimulation specifically enhances the emotional recognition of facial anger and sadness. *Cognition and Emotion, 26*(5), 786–799. https://doi.org/10.1080/02699931.2011.619520

Fett, A. K., Viechtbauer, W., Dominguez, M. D., Penn, D. L., van Os, J., & Krabbendam, L. (2011). The relationship between neurocognition and social cognition with functional outcomes in schizophrenia: A meta-analysis. *Neuroscience & Biobehavioral Reviews, 35*(3), 573-588. https://doi.org/10.1016/j.neubiorev.2010.07.001

Fiez, J. A., & Raichle, M. E. (1997). Linguistic processing. *International Review of Neurobiology, 41*, 233-254. https://doi.org/10.1016/s0074-7742(08)60354-2

Flavell, J. H., Flavell, E. R., & Green, F. L. (1983). Development of the appearance-reality distinction. *Cognitive Psychology, 15*(1), 95-120. https://doi.org/10.1016/0010-0285(83)90005-1

Fletcher, P. C., Happé, F., Frith, U., Baker, S. C., Dolan, R. J., Frackowiak, R. S., & Frith, C. D. (1995). Other minds in the brain: A functional imaging study of "theory of mind" in story comprehension. *Cognition, 57*(2), 109–128. https://doi.org/10.1016/0010-0277(95)00692-R

Frith, C. D. (2004). Schizophrenia and theory of mind. *Psychological Medicine, 34*(3), 385-389. https://doi.org/10.1017/s0033291703001326

Frith, C. D. (2008). Social cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences, 363*(1499), 2033–2039. https://doi.org/10.1098/rstb.2008.0005

Frith, C. D. & Frith, U. (1991). Elective affinities in schizophrenia and childhood autism. In Social Psychiatry : Theory, Methodology, and Practice (ed. P. E. Bebbington), pp. 65–88. Transaction Publish- ers: New Brunswick, NJ.

Frith, C. D., & Corcoran, R. (1996). Exploring ‘theory of mind’ in people with schizophrenia. *Psychological Medicine, 26*(3), 521-530. https://doi.org/10.1017/s0033291700035601

Frith, C. D., & Frith, U. (2007). Social cognition in humans. *Current Biology, 17*(16), R724-R732. https://doi.org/10.1016/j.cub.2007.05.068

Frith, Chris & Frith, Uta. (2021). *Mapping Mentalizing in the Brain. 10.1007/978-3-030-51890-5_2.*

Frith, U., & Frith, C. (2010). The social brain: allowing humans to boldly go where no other species has been. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1537), 165-176.

Frith, U., & Frith, C. D. (2003). Development and neurophysiology of mentalizing. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 358*(1431), 459-473.

Fusar-Poli, P., Placentino, A., Carletti, F., Landi, P., Allen, P., Surguladze, S., Benedetti, F., Abbamonte, M., Gasparotti, R., Barale, F., Perez, J., McGuire, P., & Politi, P. (2009). Functional atlas of emotional faces processing: A voxel-based meta-analysis of 105 functional magnetic resonance imaging studies. *Journal of Psychiatry & Neuroscience, 34*(6), 418-432. PMCID: PMC2783433.

Gallese, V., Keysers, C., & Rizzolatti, G. (2004). A unifying view of the basis of social cognition. *Trends in Cognitive Sciences, 8*(9), 396-403. https://doi.org/10.1016/j.tics.2004.07.002

Glickstein, M., Strata, P., & Voogd, J. (2009). Cerebellum: History. *Neuroscience, 162*(3), 549–559 doi: 10.1016/j.neuroscience.2009.02.054. Epub 2009 Mar 9. PMID: 19272426.

Glickstein, M., Sultan, F., & Voogd, J. (2011). Functional localization in the cerebellum. *Cortex, 47*(1), 59-80. https://doi.org/10.1016/j.cortex.2009.09.001

Gregory, C., Lough, S., Stone, V., Erzinclioglu, S., Martin, L., Baron‐Cohen, S., & Hodges, J. R. (2002). Theory of mind in patients with frontal variant frontotemporal dementia and Alzheimer’s disease: theoretical and practical implications. *Brain*, *125*(4), 752-764.

Greicius, M. D., Krasnow, B., Reiss, A. L., & Menon, V. (2003). Functional connectivity in the resting brain: A network analysis of the default mode hypothesis. *Proceedings of the National Academy of Sciences, 100*(1), 253-258. https://doi.org/10.1073/pnas.0135058100

Gruol, D. L., Koibuchi, N., Manto, M., Molinari, M., Schmahmann, J. D., & Shen, Y. (2016) (Eds.), *Essentials of cerebellum and cerebellar disorders: A primer for graduate students.* Springer.

Guell, X., Hoche, F., & Schmahmann, J. D. (2015). Metalinguistic deficits in patients with cerebellar dysfunction: Empirical support for the dysmetria of thought theory. *Cerebellum, 14*(1), 50–58. https://doi.org/10.1007/s12311-014-0630-z

Guevara, E. E., Hopkins, W. D., Hof, P. R., Ely, J. J., Bradley, B. J., & Sherwood, C. C. (2021). Comparative analysis reveals distinctive epigenetic features of the human cerebellum. *PLoS Genetics, 17*(5), e1009506. https://doi.org/10.1371/journal.pgen.1009506

Habas, C., Manto, M., & Cabaraux, P. (2019). The cerebellar thalamus. *The Cerebellum, 18*(6), 1022-1035. https://doi.org/10.1007/s12311-019-01019-3

Hamilton, N. G., Frick, R. B., Takahashi, T., & Hopping, M. W. (1983). Psychiatric symptoms and cerebellar pathology. *American Journal of Psychiatry, 140*(10), 1322-1326. https://doi.org/10.1176/ajp.140.10.1322

Hanajima, R., Wang, R., Nakatani-Enomoto, S., Hamada, M., Terao, Y., Furubayashi, T., Okabe, S., Inomata-Terada, S., Yugeta, A., Rothwell, J. C., & Ugawa, Y. (2007). Comparison of different methods for estimating motor threshold with transcranial magnetic stimulation. *Clinical Neurophysiology, 118*(9), 2120-2122. https://doi.org/10.1016/j.clinph.2007.05.067

Heath, R. G., Franklin, D. E., & Shraberg, D. (1979). Gross pathology of the cerebellum in patients diagnosed and treated as functional psychiatric disorders. *Journal of Nervous and Mental Disease, 167*(10), 585-592. https://doi.org/10.1097/00005053-197910000-00001

Heider, F., & Simmel, M. (1944). An experimental study of apparent behavior. *The American Journal of Psychology, 57*(2), 243–259. https://doi.org/10.2307/1416950

Heleven, E., van Dun, K., & Van Overwalle, F. (2019). The posterior cerebellum is involved in constructing social action sequences: An fMRI study. *Scientific Reports, 9*, 11110. https://doi.org/10.1038/s41598-019-46962-7

Hezel, D. M., & McNally, R. J. (2014). Theory of mind impairments in social anxiety disorder. *Behavior Therapy, 45*(4), 530-540. https://doi.org/10.1016/j.beth.2014.02.010

Hollebrandse, B., van Hout, A. M. H., & Hendriks, P. (2011). First and second-order false belief reasoning: Does language support reasoning about the beliefs of others? In J. van Eijck

& R. Verbrugge (Eds.), *Proceedings of the Workshop on Reasoning About Other Minds: Logical and Cognitive Perspectives (RAOM-2011)* (Vol. 751, pp. 93-107). CEUR Workshop Proceedings.

Hollebrandse, B., Van Hout, A., & Hendriks, P. (2011). First and second-order false-belief reasoning: Does language support reasoning about the beliefs of others. In *CEUR Workshop Proc*(Vol. 751, pp. 93-107).

Holmes, G. (1917). The symptoms of acute cerebellar injuries due to gunshot injuries. *Brain, 40*(4), 461-535. https://doi.org/10.1093/brain/40.4.461

Hull, C., & Regehr, W. G. (2022). The cerebellar cortex. *Annual Review of Neuroscience, 45*, 151–175. https://doi.org/10.1146/annurev-neuro-091421-125115

Imaizumi, S., Mori, K., Kiritani, S., Kawashima, R., Sugiura, M., Fukuda, H., Itoh, K., Kato, T., Nakamura, A., Hatano, K., Kojima, S., & Nakamura, K. (1997). Vocal identification of speaker and emotion activates different brain regions. *NeuroReport, 8*(12), 2809-2812. https://doi.org/10.1097/00001756-199708180-00031

Ito, M. (2006). Cerebellar circuitry as a neuronal machine. *Progress in Neurobiology, 78*(3–5), 272–303. https://doi.org/10.1016/j.pneurobio.2006.02.006

Ito, M. (2008). Control of mental activities by internal models in the cerebellum. *Nature Reviews Neuroscience, 9*(4), 304–313. https://doi.org/10.1038/nrn2332

Ito, M., *The Cerebellum and Neural Control* (1984).

Ivry, R. (1993). Cerebellar involvement in the explicit representation of temporal information. *Annals of the New York Academy of Sciences, 682*, 214-230. https://doi.org/10.1111/j.1749-6632.1993.tb22970.x

Jenkins, L. M., Andrewes, D. G., Nicholas, C. L., Drummond, K. J., Moffat, B. A., Phal, P., Desmond, P., & Kessels, R. P. C. (2014). Social cognition in patients following surgery to the prefrontal cortex. *Psychiatry Research: Neuroimaging, 224*(3), 192-203. https://doi.org/10.1016/j.pscychresns.2014.08.007

Kalbe, E., Schlegel, M., Sack, A. T., Nowak, D. A., Dafotakis, M., Bangard, C., Brand, M., Shamay-Tsoory, S., Onur, O. A., & Kessler, J. (2010). Dissociating cognitive from affective theory of mind: A TMS study. *Cortex, 46*(6), 769-780. https://doi.org/10.1016/j.cortex.2009.07.010

Kang, S., Jun, S., Baek, S. J., Park, H., Yamamoto, Y., & Tanaka-Yamamoto, K. (2021). Recent advances in the understanding of specific efferent pathways emerging from the cerebellum. *Frontiers in Neuroanatomy, 15*, Article 759948. https://doi.org/10.3389/fnana.2021.759948

Katsetos, C. D., Hyde, T. M., & Herman, M. M. (1997). Neuropathology of the cerebellum in schizophrenia—An update: 1996 and future directions. *Biological Psychiatry, 42*(3), 213-224. https://doi.org/10.1016/S0006-3223(96)00313-7

Kebschull, J. M., Casoni, F., Consalez, G. G., Goldowitz, D., Hawkes, R., Ruigrok, T. J. H., Schilling, K., Wingate, R., Wu, J., Yeung, J., & Uusisaari, M. Y. (2024). Cerebellum lecture: The cerebellar nuclei—Core of the cerebellum. *Cerebellum, 23*(2), 620–677. https://doi.org/10.1007/s12311-022-01506-0

Kelly, R. M., & Strick, P. L. (2003). Cerebellar loops with motor cortex and prefrontal cortex of a nonhuman primate. *Journal of Neuroscience, 23*(23), 8432–8444. https://doi.org/10.1523/JNEUROSCI.23-23-08432.2003

Keren-Happuch, E., Chen, S.-H. A., Ho, M.-H. R., & Desmond, J. E. (2014). A meta-analysis of cerebellar contributions to higher cognition from PET and fMRI studies. *Human Brain Mapping, 35*(2), 593-615. https://doi.org/10.1002/hbm.22194

Kerr, N., Dunbar, R. I., & Bentall, R. P. (2003). Theory of mind deficits in bipolar affective disorder. *Journal of affective disorders*, *73*(3), 253-259.

Koch G, Oliveri M, Torriero S, Salerno S, Lo Gerfo E, Caltagirone C. Repetitive TMS of cerebellum interferes with millisecond time processing. Exp Brain Res. 2007 May;179(2):291-9. doi: 10.1007/s00221-006-0791-1. Epub 2006 Dec 5. PMID: 17146647.

Koziol, L. F., Budding, D., Andreasen, N., D'Arrigo, S., Bulgheroni, S., Imamizu, H., Ito, M., Manto, M., Marvel, C., Parker, K., Pezzulo, G., Ramnani, N., Riva, D., Schmahmann, J., Vandervert, L., & Yamazaki, T. (2014). Consensus paper: The cerebellum's role in movement and cognition. *Cerebellum, 13*(1), 151-177. https://doi.org/10.1007/s12311-013-0511-x

Krause, L., Enticott, P. G., Zangen, A., & Fitzgerald, P. B. (2012). The role of medial prefrontal cortex in theory of mind: A deep rTMS study. *Behavioural Brain Research, 228*(1), 87-90. https://doi.org/10.1016/j.bbr.2011.11.037

Küper, M., Hermsdörfer, J., Brandauer, B., Thürling, M., Schoch, B., Theysohn, N., & Timmann, D. (2011). Lesions of the dentate and interposed nuclei are associated with impaired prehension in cerebellar patients. *Neuroscience Letters, 499*(2), 132-136. https://doi.org/10.1016/j.neulet.2011.05.055

Lee, K. H., Farrow, T. F., Spence, S. A., & Woodruff, P. W. (2004). Social cognition, brain networks and schizophrenia. *Psychological Medicine, 34*(3), 391-400. https://doi.org/10.1017/s0033291703001284

Leggio, M. G., Chiricozzi, F. R., Clausi, S., Tedesco, A. M., & Molinari, M. (2011). The neuropsychological profile of cerebellar damage: The sequencing hypothesis. *Cortex, 47*(2), 137–144. https://doi.org/10.1016/j.cortex.2009.08.011

Leggio, M., & Molinari, M. (2015). Cerebellar sequencing: A trick for predicting the future. *Cerebellum, 14*(1), 35–38. https://doi.org/10.1007/s12311-014-0616-x

Leggio, M., & Olivito, G. (2018). Topography of the cerebellum in relation to social brain regions and emotions. *Handbook of Clinical Neurology, 154*, 71-84. https://doi.org/10.1016/B978-0-444-63956-1.00005-9

Lent, R., Azevedo, F. A. C., Andrade-Moraes, C. H., & Pinto, A. V. O. (2012). How many neurons do you have? Some dogmas of quantitative neuroscience under revision. *European Journal of Neuroscience, 35*(1), 1–9. https://doi.org/10.1111/j.1460-9568.2011.07923.x

Leslie, A. M., & Frith, U. (1987). Metarepresentation and autism: How not to lose one's marbles. *Cognition, 27*(3), 291-294. https://doi.org/10.1016/S0010-0277(87)80014-8

Liang YS, Zhou SZ, Zhang YJ, et al.: Altered empathy-related resting-state functional connectivity in patients with bipolar disorder. Eur Arch Psychiatry Clin Neurosci. 2022, 272:839-48. 10.1007/s00406-021- 01305-4

Lupo, M., Olivito, G., Gragnani, A., Saettoni, M., Siciliano, L., Pancheri, C., Panfili, M., Bozzali, M., Delle Chiaie, R., & Leggio, M. (2021). Comparison of cerebellar grey matter alterations in bipolar and cerebellar patients: Evidence from voxel-based analysis. *International Journal of Molecular Sciences, 22*(7), 3511. https://doi.org/10.3390/ijms22073511

Ma, Q., Pu, M., Heleven, E., Haihambo, N. P., Baetens, K., Baeken, C., Deroost, N., & Van Overwalle, F. (2021). The posterior cerebellum supports implicit learning of social belief sequences. *Cognitive, Affective, & Behavioral Neuroscience, 21*(5), 970-992. https://doi.org/10.3758/s13415-021-00910-z

Malatesta, G., D'Anselmo, A., Prete, G., & et al. (2024). The predictive role of the posterior cerebellum in the processing of dynamic emotions. *Cerebellum, 23*, 545–553. https://doi.org/10.1007/s12311-023-01574-w

Manto, M., Haines, D. Cerebellar Research: Two Centuries of Discoveries. *Cerebellum* 11, 446–448 (2012). https://doi.org/10.1007/s12311-011-0336-4

Marr, D. (1969). A theory of cerebellar cortex. *Journal of Physiology, 202*(2), 437-470. https://doi.org/10.1113/jphysiol.1969.sp008820

Mars, R. B., Neubert, F. X., Noonan, M. P., Sallet, J., Toni, I., & Rushworth, M. F. (2012). On the relationship between the "default mode network" and the "social brain." *Frontiers in Human Neuroscience, 6*, 189. https://doi.org/10.3389/fnhum.2012.00189

Marvel, C. L., & Desmond, J. E. (2010). Functional topography of the cerebellum in verbal working memory. *Neuropsychology Review, 20*(3), 271-279. https://doi.org/10.1007/s11065-010-9137-7

Metoki, A., Wang, Y., & Olson, I. R. (2022). The social cerebellum: A large-scale investigation of functional and structural specificity and connectivity. *Cerebral Cortex, 32*(5), 987–1003. https://doi.org/10.1093/cercor/bhab260

Middleton, F. A., & Strick, P. L. (2000). Basal ganglia and cerebellar loops: Motor and cognitive circuits. *Brain Research Reviews, 31*(2-3), 236-250. https://doi.org/10.1016/S0165-0173(99)00040-5

Molenberghs, P., Cunnington, R., & Mattingley, J. B. (2012). Brain regions with mirror properties: A meta-analysis of 125 human fMRI studies. *Neuroscience & Biobehavioral Reviews, 36*(1), 341-349. https://doi.org/10.1016/j.neubiorev.2011.07.004

Montgomery, D. E., & Montgomery, D. A. (1999). The influence of movement and outcome on young children's attributions of intention. *British Journal of Developmental Psychology, 17*(2), 245-261. https://doi.org/10.1348/026151099165258

Morton, S. M., & Bastian, A. J. (2004). Cerebellar control of balance and locomotion. *Neuroscientist, 10*(3), 247-259. https://doi.org/10.1177/1073858404263517

Nashef, A., Cohen, O., Harel, R., Israel, Z., & Prut, Y. (2019). Reversible block of cerebellar outflow reveals cortical circuitry for motor coordination. *Cell Reports, 27*(9), 2608-2619.e4. https://doi.org/10.1016/j.celrep.2019.04.100

Nashef, A., Mitelman, R., Harel, R., & Prut, Y. (2021). Area-specific thalamocortical synchronization underlies the transition from motor planning to execution. *Proceedings of the National Academy of Sciences, 118*(6), e2012658118. https://doi.org/10.1073/pnas.2012658118x

Németh, N., Mátrai, P., Hegyi, P., Czéh, B., Czopf, L., Hussain, A., Pammer, J., Szabó, I., Solymár, M., Kiss, L., Hartmann, P., Szilágyi, Á. L., Kiss, Z., & Simon, M. (2018). Theory of mind disturbances in borderline personality disorder: A meta-analysis. *Psychiatry Research, 270*, 143-153. https://doi.org/10.1016/j.psychres.2018.08.049

Nitschke, M. F., Arp, T., Stavrou, G., Erdmann, C., & Heide, W. (2005). The cerebellum in the cerebro-cerebellar network for the control of eye and hand movements — An fMRI study. *Progress in Brain Research, 148*, 151–164. Elsevier. https://doi.org/10.1016/S0079-6123(04)48013-3

Nobre, A. C., Gitelman, D. R., Dias, E. C., & Mesulam, M. M. (2000). Covert visual spatial orienting and saccades: Overlapping neural systems. *NeuroImage, 11*(3), 210–216. https://doi.org/10.1006/nimg.2000.0539

Noda, H., & Fujikado, T. (1987). Topography of the oculomotor area of the cerebellar vermis in macaques as determined by microstimulation. *Journal of Neurophysiology, 58*(2), 359–378. https://doi.org/10.1152/jn.1987.58.2.359

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*(1), 97-113. https://doi.org/10.1016/0028-3932(71)90067-4

Olivito, G., Lupo, M., Laghi, F., Clausi, S., Baiocco, R., Cercignani, M., Bozzali, M., & Leggio, M. (2018). Lobular patterns of cerebellar resting-state connectivity in adults with autism spectrum disorder. *European Journal of Neuroscience, 47*(6), 729-735. https://doi.org/10.1111/ejn.13752

Oostland, M., & van Hooft, J. A. (2013). The role of serotonin in cerebellar development. *Neuroscience, 248*, 201-212. https://doi.org/10.1016/j.neuroscience.2013.05.029

Ozgen, M.N., Sahin, N.E., Ertan, N. *et al.* Investigation of total cerebellar and flocculonodular lobe volume in Parkinson’s disease and healthy individuals: a brain segmentation study. *Neurol Sci* 45, 4291–4298 (2024). https://doi.org/10.1007/s10072-024-07509-5

Palesi, F., Lorenzi, R. M., Casellato, C., Ritter, P., Jirsa, V., Gandini Wheeler-Kingshott, C. A. M., & D'Angelo, E. (2020). The importance of cerebellar connectivity on simulated brain dynamics. *Frontiers in Cellular Neuroscience, 14*, Article 240. https://doi.org/10.3389/fncel.2020.00240

Pannese, E. (1999). The Golgi stain: Invention, diffusion, and impact on neurosciences. *Journal of the History of the Neurosciences, 8*(2), 132–140. https://doi.org/10.1076/jhin.8.2.132.1847. PMID: 11624294.

Paulesu, E., Frith, C. D., & Frackowiak, R. S. (1993). The neural correlates of the verbal component of working memory. *Nature, 362*(6418), 342–345.

Pelphrey, K. A., Morris, J. P., & McCarthy, G. (2004). Grasping the intentions of others: The perceived intentionality of an action influences activity in the superior temporal sulcus during social perception. *Journal of Cognitive Neuroscience, 16*(10), 1706-1716. https://doi.org/10.1162/0898929042947900

Perner, J., & Wimmer, H. (1985). “John thinks that Mary thinks that…” attribution of second-order beliefs by 5-to 10-year-old children. *Journal of experimental child psychology*, *39*(3), 437-471.

Perner, J., Leekam, S. R., & Wimmer, H. (1987). Three-year-olds’ difficulty with false belief: The case for a conceptual deficit. *British Journal of Developmental Psychology, 5*(2), 125-137. https://doi.org/10.1111/j.2044-835X.1987.tb01048.x

Pezzetta, R., Gambarota, F., Tarantino, V., Devita, M., Cattaneo, Z., Arcara, G., Mapelli, D., & Masina, F. (2024). A meta-analysis of non-invasive brain stimulation (NIBS) effects on cerebellar-associated cognitive processes. *Neuroscience & Biobehavioral Reviews, 157*, 105509. https://doi.org/10.1016/j.neubiorev.2023.105509

Pierce, J. E., Thomasson, M., Voruz, P., & et al. (2023). Explicit and implicit emotion processing in the cerebellum: A meta-analysis and systematic review. *Cerebellum, 22*, 852–864. https://doi.org/10.1007/s12311-022-01459-4

Ponce, G. V., Klaus, J., & Schutter, D. J. L. G. (2022). A brief history of cerebellar neurostimulation. *The Cerebellum, 21*(4), 715–730. https://doi.org/10.1007/s12311-021-01310-2

Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences, 1*(4), 515-526. https://doi.org/10.1017/S0140525X00076512

Prsa, M., & Thier, P. (2022). Cerebellum: Eye movements. In D. W. Pfaff, N. D. Volkow, & J. L. Rubenstein (Eds.), *Neuroscience in the 21st century*. Springer, Cham. https://doi.org/10.1007/978-3-030-88832-9_39

Pylyshyn, Zenon W. (1978). When is attribution of beliefs justified? [P&W]. Behavioral and Brain Sciences 1 (4):592-593.

Raichle, M. E., MacLeod, A. M., Snyder, A. Z., & Shulman, G. L. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences, 98*(2), 676-682. https://doi.org/10.1073/pnas.98.2.676

Rawson, N. R. (1932). The story of the cerebellum. *Canadian Medical Association Journal, 26*(2), 220-225.

Ritchie, L. (1976). Effects of cerebellar lesions on saccadic eye movements. *Journal of Neurophysiology, 39*(6), 1246-1256. https://doi.org/10.1152/jn.1976.39.6.1246

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience, 27*, 169-192. https://doi.org/10.1146/annurev.neuro.27.070203.144230

Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Brain Research. Cognitive Brain Research, 3*(2), 131-141. https://doi.org/10.1016/0926-6410(95)00038-0

Rossetto, F., Castelli, I., Baglio, F., Massaro, D., Alberoni, M., Nemni, R., Shamay-Tsoory, S., & Marchetti, A. (2018). Cognitive and affective theory of mind in mild cognitive impairment and Parkinson's disease: Preliminary evidence from the Italian version of the Yoni task. *Developmental Neuropsychology, 43*(8), 764-780. https://doi.org/10.1080/87565641.2018.1529175

Rossi, S., Hallett, M., Rossini, P. M., & Pascual-Leone, A. (2011). Screening questionnaire before TMS: An update. *Clinical Neurophysiology, 122*(8), 1686. https://doi.org/10.1016/j.clinph.2010.12.037

Roth, R. M., & Saykin, A. J. (2004). Executive dysfunction in attention-deficit/hyperactivity disorder: Cognitive and neuroimaging findings. *Psychiatric Clinics of North America, 27*(1), 83-96, ix. https://doi.org/10.1016/S0193-953X(03)00112-6

Rueckriegel, S. M., Blankenburg, F., Henze, G., Baqué, H., & Driever, P. H. (2009). Loss of fine motor function correlates with ataxia and decline of cognition in cerebellar tumor survivors. *Pediatric Blood & Cancer, 53*(3), 424-431. https://doi.org/10.1002/pbc.22104

Ruitenberg, M. F. L., Santens, P., & Notebaert, W. (2020). Cognitive and affective theory of mind in healthy aging. *Experimental Aging Research, 46*(5), 382-395. https://doi.org/10.1080/0361073X.2020.1802980

Salman, M. S., & Tsai, P. (2016). The role of the pediatric cerebellum in motor functions, cognition, and behavior: A clinical perspective. *Neuroimaging Clinics of North America, 26*(3), 317-329. https://doi.org/10.1016/j.nic.2016.03.003

Sapolsky, R. M. (2017). *Behave: The biology of humans at our best and worst*. Penguin Books.

Saxe, R. (2006). Uniquely human social cognition. *Current Opinion in Neurobiology, 16*(2), 235-239. https://doi.org/10.1016/j.conb.2006.03.001

Saxe, R., Xiao, D. K., Kovacs, G., Perrett, D. I., & Kanwisher, N. (2004). A region of right posterior superior temporal sulcus responds to observed intentional actions. *Neuropsychologia, 42*(11), 1435-1446. https://doi.org/10.1016/j.neuropsychologia.2004.04.015

Schmahmann, J. D. (1991). An emerging concept: The cerebellar contribution to higher function. *Archives of Neurology, 48*(11), 1178-1187. https://doi.org/10.1001/archneur.1991.00530230086029

Schmahmann, J. D. (1996). From movement to thought: Anatomic substrates of the cerebellar contribution to cognitive processing. *Human Brain Mapping, 4*(3), 174-198. https://doi.org/10.1002/(SICI)1097-0193(1996)4:3<174::AID-HBM3>3.0.CO;2-0

Schmahmann, J. D. (2010). The role of the cerebellum in cognition and emotion: Personal reflections since 1982 on the dysmetria of thought hypothesis, and its historical evolution from theory to therapy. *Neuropsychology Review, 20*(3), 236-260. https://doi.org/10.1007/s11065-010-9142-x

Schmahmann, J. D. (2019). The cerebellum and cognition. *Neuroscience Letters, 688,* 62–75. https://doi.org/10.1016/j.neulet.2018.07.005

Schmahmann, J. D., & Sherman, J. C. (1998). The cerebellar cognitive affective syndrome. *Brain, 121*(Pt 4), 561–579. https://doi.org/10.1093/brain/121.4.561

Schmahmann, J. D., Guell, X., Stoodley, C. J., & Halko, M. A. (2019). The theory and neuroscience of cerebellar cognition. *Annual Review of Neuroscience, 42*, 337–364. https://doi.org/10.1146/annurev-neuro-070918-050258

Schmahmann, J. D., Weilburg, J. B., & Sherman, J. C. (2007). The neuropsychiatry of the cerebellum - Insights from the clinic. *The Cerebellum, 6*(3), 254–267. https://doi.org/10.1080/14734220701490995

Sereno, M. I., Diedrichsen, J., Tachrount, M., Testa-Silva, G., d'Arceuil, H., & De Zeeuw, C. (2020). The human cerebellum has almost 80% of the surface area of the neocortex. *Proceedings of the National Academy of Sciences of the United States of America, 117*(32), 19538–19543. https://doi.org/10.1073/pnas.2002896117

Shamay-Tsoory, S. G., & Aharon-Peretz, J. (2007). Dissociable prefrontal networks for cognitive and affective theory of mind: A lesion study. *Neuropsychologia, 45*(13), 3054-3067. https://doi.org/10.1016/j.neuropsychologia.2007.05.021

Shamay-Tsoory, S. G., Harari, H., Aharon-Peretz, J., & Levkovitz, Y. (2010). The role of the orbitofrontal cortex in affective theory of mind deficits in criminal offenders with psychopathic tendencies. *Cortex, 46*(5), 668-677. https://doi.org/10.1016/j.cortex.2009.04.008

Shamay-Tsoory, S. G., Shur, S., Barcai-Goodman, L., Medlovich, S., Harari, H., & Levkovitz, Y. (2007). Dissociation of cognitive from affective components of theory of mind in schizophrenia. *Psychiatry Research, 149*(1-3), 11-23. https://doi.org/10.1016/j.psychres.2005.10.018

Shamay-Tsoory, S. G., Tibi-Elhanany, Y., & Aharon-Peretz, J. (2006). The ventromedial prefrontal cortex is involved in understanding affective but not cognitive theory of mind stories. *Social Neuroscience, 1*(3-4), 149-166. https://doi.org/10.1080/17470910600985589

Shamay-Tsoory, S. G., Tomer, R., Berger, B. D., Goldsher, D., & Aharon-Peretz, J. (2005). Impaired "affective theory of mind" is associated with right ventromedial prefrontal damage. *Cognitive and Behavioral Neurology, 18*(1), 55-67. https://doi.org/10.1097/01.wnn.0000152228.90129.99

Shinn, A. K., Roh, Y. S., Ravichandran, C. T., Baker, J. T., Öngür, D., & Cohen, B. M. (2017). Aberrant cerebellar connectivity in bipolar disorder with psychosis. *Biological Psychiatry: Cognitive Neuroscience and Neuroimaging, 2*(5), 438-448. https://doi.org/10.1016/j.bpsc.2016.07.002

Shinoda, Y., Kakei, S., Futami, T., & Wannier, T. (1993). Thalamocortical organization in the cerebello-thalamo-cortical system. *Cerebral Cortex, 3*(5), 421–429. https://doi.org/10.1093/cercor/3.5.421

Shulman GL, Fiez JA, Corbetta M, Buckner RL, Miezin FM, Raichle ME, Petersen SE (1997) Common blood flow changes across visual tasks: II. Decreases in cerebral cortex. J Cogn Neurosci 9:648 – 663.

Sillitoe, R. V., Fu, Y., & Watson, C. (2012). Cerebellum. In C. Watson, G. Paxinos, & L. Puelles (Eds.), *The mouse nervous system* (pp. 360–397). Elsevier Academic Press. https://doi.org/10.1016/B978-0-12-369497-3.10011-1

Silston, B., Bassett, D. S., & Mobbs, D. (2018). How dynamic brain networks tune social behavior in real time. *Current Directions in Psychological Science, 27*(6), 413-421. https://doi.org/10.1177/0963721418773362

Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R. J., & Frith, C. D. (2004). Empathy for pain involves the affective but not sensory components of pain. *Science, 303*(5661), 1157-1162. https://doi.org/10.1126/science.1093535

Singh, R. (2021). Cerebellum: Its anatomy, functions, and diseases. In *IntechOpen*. https://doi.org/10.5772/intechopen.93064

Smaers, J. B., Turner, A. H., Gómez-Robles, A., & Sherwood, C. C. (2018). A cerebellar substrate for cognition evolved multiple times independently in mammals. *eLife, 7*, Article e35696. https://doi.org/10.7554/eLife.35696

Smallwood, J., Bernhardt, B. C., Leech, R., Bzdok, D., Jefferies, E., & Margulies, D. S. (2021). The default mode network in cognition: a topographical perspective. *Nature reviews neuroscience*, *22*(8), 503-513.

Sokolov, A. A., Miall, R. C., & Ivry, R. B. (2017). The cerebellum: Adaptive prediction for movement and cognition. *Trends in Cognitive Sciences, 21*(5), 313–332. https://doi.org/10.1016/j.tics.2017.02.005

Sotelo, C. (2008). Viewing the cerebellum through the eyes of Ramón y Cajal. *Cerebellum, 7*(4), 517–522. https://doi.org/10.1007/s12311-008-0078-0. PMID: 18972180.

Sotelo, C. (2010). Nature over nurture (Commentary on Rolando et al.). *European Journal of Neuroscience, 31*(7), 1339-1339. https://doi.org/10.1111/j.1460-9568.2010.07234.x

Sotelo, C. (2011). Camillo Golgi and Santiago Ramón y Cajal: The anatomical organization of the cortex of the cerebellum. Can the neuron doctrine still support our actual knowledge on the cerebellar structural arrangement? *Brain Research Reviews, 66*(1–2), 16–34. https://doi.org/10.1016/j.brainresrev.2010.05.004

Spencer, R. M. C., & Ivry, R. B. (2013). Cerebellum and timing. In *Handbook of the cerebellum and cerebellar disorders*(pp. 1201–1219). Springer. https://doi.org/10.1007/978-94-007-1333-8_52

Springer, K., Meier, J. A., & Berry, D. S. (1996). Nonverbal bases of social perception: Developmental change in sensitivity to patterns of motion that reveal interpersonal events. *Journal of Nonverbal Behavior, 20*, 199–211. https://doi.org/10.1007/BF02248673

Stone, V. E., Baron-Cohen, S., & Knight, R. T. (1998). Frontal lobe contributions to theory of mind. *Journal of Cognitive Neuroscience, 10*(5), 640-656. https://doi.org/10.1162/089892998562942

Stoodley, C. J., & Schmahmann, J. D. (2009). Functional topography in the human cerebellum: A meta-analysis of neuroimaging studies. *NeuroImage, 44*(2), 489-501. https://doi.org/10.1016/j.neuroimage.2008.08.039

Stoodley, C. J., & Schmahmann, J. D. (2018). Functional topography of the human cerebellum. In *Handbook of Clinical Neurology* (Vol. 154, pp. 59–70). Elsevier. https://doi.org/10.1016/B978-0-444-63956-1.00004-7

Stout, D., & Hecht, E. E. (2017). Evolutionary neuroscience of cumulative culture. *Proceedings of the National Academy of Sciences, 114*(30), 7861-7868. https://doi.org/10.1073/pnas.1620738114

Strick, P. L., Dum, R. P., & Fiez, J. A. (2009). Cerebellum and nonmotor function. *Annual Review of Neuroscience, 32*(1), 413–434. https://doi.org/10.1146/annurev.neuro.31.060407.125606

Tai, H., Kandeel, N., Menon, M., Ibrahim, A., Choo, B., Santana, R., & Jolayemi, A. (2024). Role of the cerebellum in bipolar disorder: A systematic literature review. *Cureus, 16*(3), e56044. https://doi.org/10.7759/cureus.56044

Takahashi, M., & Shinoda, Y. (2021). Neural circuits of inputs and outputs of the cerebellar cortex and nuclei. *Neuroscience, 462*, 70–88. https://doi.org/10.1016/j.neuroscience.2020.07.051

Talairach, J., & Tournoux, P. (1998). *Co-planar stereotaxic atlas of the human brain: 3-dimensional proportional system: An approach to cerebral imaging*. Thieme Medical Publishers, Inc.

Talati, A., Pantazatos, S. P., Schneier, F. R., Weissman, M. M., & Hirsch, J. (2013). Gray matter abnormalities in social anxiety disorder: Primary, replication, and specificity studies. *Biological Psychiatry, 73*(1), 75-84. https://doi.org/10.1016/j.biopsych.2012.05.022

Tesche, C. D., & Karhu, J. J. (2000). Anticipatory cerebellar responses during somatosensory omission in man. *Human Brain Mapping, 9*(3), 119-142. https://doi.org/10.1002/(SICI)1097-0193(200003)9:3<119::AID-HBM2>3.0.CO;2-R

Théoret, H., Haque, J., & Pascual-Leone, A. (2001). Increased variability of paced finger tapping accuracy following repetitive magnetic stimulation of the cerebellum in humans. *Neuroscience Letters, 306*(1-2), 29-32. https://doi.org/10.1016/s0304-3940(01)01860-2

Timmann, D., & Daum, I. (2007). Cerebellar contributions to cognitive functions: A progress report after two decades of research. *Cerebellum, 6*(3), 159–162. https://doi.org/10.1080/14734220701496448

Unverdi, M., & Alsayouri, K. (2023). Neuroanatomy, cerebellar dysfunction. In *StatPearls [Internet]*. StatPearls Publishing. https://www.ncbi.nlm.nih.gov/books/NBK542295/

Van Essen, D. C., Donahue, C. J., & Glasser, M. F. (2018). *Development and evolution of cerebral and cerebellar cortex*. Brain, Behavior and Evolution, 91(3), 158–169. https://doi.org/10.1159/000489943

Van Overwalle, F. (2009). Social cognition and the brain: A meta-analysis. *Human Brain Mapping, 30*(3), 829-858. https://doi.org/10.1002/hbm.20547

Van Overwalle, F., Baetens, K., Mariën, P., & Vandekerckhove, M. (2015a). Cerebellar areas dedicated to social cognition? A comparison of meta-analytic and connectivity results. *Social Neuroscience, 10*(4), 337-344. https://doi.org/10.1080/17470919.2015.1005666

Van Overwalle, F., D'Aes, T., & Mariën, P. (2015). Social cognition and the cerebellum: A meta-analytic connectivity analysis. *Human Brain Mapping, 36*(12), 5137-5154. https://doi.org/10.1002/hbm.23002

Van Overwalle, F., Baetens, K., Mariën, P., & Vandekerckhove, M. (2014). Social cognition and the cerebellum: A meta-analysis of over 350 fMRI studies. *NeuroImage, 86*, 554–572. https://doi.org/10.1016/j.neuroimage.2013.09.033

Van Overwalle, F., & Baetens, K. (2009). Understanding others' actions and goals by mirror and mentalizing systems: a meta-analysis. *Neuroimage*, *48*(3), 564-584.

Van Overwalle, F., De Coninck, S., Heleven, E., Perrotta, G., Taib, N. O. B., Manto, M., & Mariën, P. (2019). The role of the cerebellum in reconstructing social action sequences: A pilot study. *Social Cognitive and Affective Neuroscience, 14*(5), 549–558. https://doi.org/10.1093/scan/nsz032

Van Overwalle, F., Ma, Q., & Heleven, E. (2020). II cerebellum is specialized for social mentalizing and emotional self-experiences: A meta-analysis. *Social Cognitive and Affective Neuroscience, 15*(9), 905–928. https://doi.org/10.1093/scan/nsaa124

Van Overwalle, F., Manto, M., Cattaneo, Z., Clausi, S., Ferrari, C., Gabrieli, J. D. E., Guell, X., Heleven, E., Lupo, M., Ma, Q., Michelutti, M., Olivito, G., Pu, M., Rice, L. C., Schmahmann, J. D., Siciliano, L., Sokolov, A. A., Stoodley, C. J., van Dun, K., Vandervert, L., & Leggio, M. (2020). Consensus paper: Cerebellum and social cognition. *Cerebellum, 19*(6), 833–868. https://doi.org/10.1007/s12311-020-01155-1

Van Overwalle, F., Pu, M., Ma, Q., Li, M., Haihambo, N., Baetens, K., Deroost, N., Baeken, C., & Heleven, E. (2022). The involvement of the posterior cerebellum in reconstructing and predicting social action sequences. *Cerebellum, 21*(5), 733–741. https://doi.org/10.1007/s12311-021-01333-9

Vandervert, L. (2016). The prominent role of the cerebellum in the learning, origin and advancement of culture. *Cerebellum & Ataxias, 3*, 10. https://doi.org/10.1186/s40673-016-0049-z

Vandervert, L. (2018). How prediction based on sequence detection in the cerebellum led to the origins of stone tools, language, and culture and, thereby, to the rise of Homo sapiens. *Frontiers in Cellular Neuroscience, 12*, 408. https://doi.org/10.3389/fncel.2018.00408

Vandervert, L., Manto, M., Adamaszek, M., Ferrari, C., Ciricugno, A., & Cattaneo, Z. (2024). The evolution of the optimization of cognitive and social functions in the cerebellum and thereby the rise of Homo sapiens through cumulative culture. *The Cerebellum*, 1-12. https://doi.org/10.1007/s12311-024-01692-z

Voogd, J., & Koehler, P. J. (2018). Historic notes on anatomic, physiologic, and clinical research on the cerebellum. *Handbook of Clinical Neurology, 154*, 3-26. https://doi.org/10.1016/B978-0-444-63956-1.00001-1

Watson, T. C., Koutsikou, S., Cerminara, N. L., Flavell, C. R., Crook, J. J., Lumb, B. M., & Apps, R. (2013). The olivo-cerebellar system and its relationship to survival circuits. *Frontiers in Neural Circuits, 7*, 72. https://doi.org/10.3389/fncir.2013.00072

Wicker, B., Keysers, C., Plailly, J., Royet, J. P., Gallese, V., & Rizzolatti, G. (2003). Both of us disgusted in my insula: The common neural basis of seeing and feeling disgust. *Neuron, 40*(3), 655-664. https://doi.org/10.1016/s0896-6273(03)00679-2

Wimmer, H., & Perner, J. (1983). Beliefs about beliefs: Representation and constraining function of wrong beliefs in young children's understanding of deception. *Cognition, 13*(1), 103-128. https://doi.org/10.1016/0010-0277(83)90004-5

Zhang, X. Y., Wang, J. J., & Zhu, J. N. (2016). Cerebellar fastigial nucleus: From anatomic construction to physiological functions. *Cerebellum & Ataxias, 3*, Article 9. https://doi.org/10.1186/s40673-016-0047-1