



Federico D'Agata and Laura Orsi

Abstract

In this chapter, after having clarified which definition of emotion we followed, starting from Darwin and evolutionary psychology, we tried to examine the main mechanisms of emotional recognition from a behavioral and cerebral point of view: emotional contagion and cognitive empathy. The link between these skills and social cognition has been discussed. We tried to understand through the description of comparative studies on animals, studies on populations with cerebellar lesions in animals and humans, neurostimulation studies, and studies on neuropsychiatric pathologies with alterations to the cerebellar networks the possible involvement of the cerebellum in these mechanisms, also investigating its possible causal role. The evidence, even if mainly of a correlational type, is numerous and robust enough to be able to affirm the existence of significant involvement of the cerebellum in social cognition and in the recognition of negative emotions, especially fear.

Keywords

Cerebellum · Social cognition · Emotion recognition · Cerebellar stroke

4.1 Some Definition about Emotion and Emotion Recognition

It is important, talking about the cerebellum and emotions, to give some definitions, but it is not easy as there does not exist a consensual definition of what emotions are, either in philosophy or in affective science (Scarantino and de Sousa 2021). It is more common, in exemplificative or prototypical descriptions, to consider emotions as intentional (directed toward something), motivating (fueling action), valenced (positive vs. negative), conscious, short-lived, preverbal, recalcitrant to reason, universal (trans-cultural and transspecies), associated with typical expressions, embodied, indicators intertwined with arousal and physiological functions (Aristotle et al. 2014; Aristotle and Lanza 1987; Damasio 1994; Descartes 2011; Descartes and Obinu 2010; Hume 1987; Lucretius Carus and Fellin 2013; Sartre and Pirillo 2004; de Spinoza et al. 2017). But their heterogeneity is huge; we can easily think counterexamples (Barrett et al. 2019) of the previous attributes: e.g., long-lived grief, unconscious fear of failing in life, without prototypical facial expression like regret,

F. D'Agata (✉)
Department of Neurosciences, University of Turin, Turin,
Italy
e-mail: federico.dagata@unito.it

L. Orsi
Department of Neurosciences, Città della Salute e della
Scienza, Turin, Italy

depending on culture like respect, exclusively human-like *schadenfreude*, and opportunistic signals of admiration or happiness.

Following the *Stanford Encyclopedia of Philosophy* (Scarantino and de Sousa 2021), it could be useful to try to describe an emotion by 5 components: evaluative (e.g., danger detection), physiological (e.g., increased heartbeat), phenomenological (e.g., uneasiness), expressive (e.g., frown), behavioral (e.g., flee), and cognitive (e.g., focus attention). We of course will be more interested in the expressive component that needs to be perceived and processed for emotion recognition, but that, in general, can be absent, hidden, or difficult to detect.

We need to answer the questions of how emotions are expressed, what is the mechanism that humans use to detect and recognize these expressions, why is it useful to identify them, and is the cerebellum necessary, important, or helpful for this task?

We can investigate the role of the cerebellum in the recognition of emotions using tools that try to map neural circuits and areas involved with invasive (e.g., microelectrode array recordings) and noninvasive techniques (e.g., magnetic resonance). Lesions or alterations in the development of cerebellar structures in both humans and animals can also help. Finally, with the comparative study between animal species, we can juxtapose cerebellar and behavioral differences.

The limitations of these tools derive from the fact that they rarely constitute causal evidence but often only correlations. Surely the most robust evidence derives from lesion studies on animal models, but they have other limitations: the communication and understanding of emotions in animals are reduced and they are often studies linked to conditioning paradigms and fear that is the emotion most simple to study and control in an experimental setting.

4.2 Emotion Recognition Mechanisms and Social Cognition

Ekman (2009) commenting on Darwin's pioneering work on emotions (Darwin and Ekman 2009) describes the 5 main contributions that he took up in his theorization: emotions are discrete, are expressed mainly through the face, are universal, are present in other species (among these Darwin mentioned horses, dogs, cats, bees, and roosters), and are "serviceable habit." This last concept is interesting, a "serviceable habit" is not a characteristic that is selected with a precise purpose, but it is simply an association between a helpful behavior and its typical expression. For example, if it can be useful in exploring space to open our eyes when we do it because we feel fear, we will begin to associate this motor reflex with the state of fear. This position has been taken up in a reinforced version by evolutionary psychologists which believe that the expression of emotions may be an adaptive behavior present in different animal species. A growing number of studies suggest that many aspects of higher-order social functions, including emotion recognition, may be present in species ranging from primates to rodents, indicating a conserved role in social animals (Ferretti and Papaleo 2019). An indicator of aggression, for example, can make the encounter between two animals less dangerous, or a signal of joy and optimism can discourage a predator. Where the social aspects become more important and complex, the ability to decipher the expressions of the conspecifics becomes essential. For example, to a group of animals in which the fear felt by one that detects a danger can alert and scare the whole group to safety (Ferretti and Papaleo 2019). In humans, it is even more complex as the emotional expression can be associated with its awareness and the understanding of other mental states, so humans can modulate, control, or simulate emotion expression, at least partially (e.g., acting), without considering the cultural and language aspects that can influence emotion expression and detection.

Two possible, non-mutually exclusive mechanisms underlying emotion recognition have been proposed: emotional contagion and cognitive empathy (Nieuwburg et al. 2021).

Emotional contagion is a rather low-level bottom-up mechanism in which the state of the observed is automatically synchronized with that of the observer by copying the expressions of others and allowing for emotional convergence. To explain the contagion, theories of simulation and imagination have sometimes been proposed (Keysers and Gazzola 2007); the cerebellum could be involved having been observed to have a role in many tasks of this type (Koziol et al. 2014). Some theories propose the mirroring or automatic copying of observed motor behaviors and physiological states (Errante and Fogassi 2020); also in this case the cerebellum could play a role by being involved in learning by association and in many simple and complex reflexes (Bracha et al. 2000).

The second mechanism, the cognitive empathy, requires the ability to recognize emotion in the observed without necessarily experiencing it (Cuff et al. 2016). The most accredited hypothesis is that it is due to a mechanism linked to the representation of the emotions of others or their mental states and that social cognition skills developed subsequently in evolution (Nieuwburg et al. 2021). Primate studies, especially on great apes and Old-World monkeys, have led to results that are difficult to interpret. On the one hand, it seems clear that both mechanisms are present in some species, but it is not possible to decipher a clear pattern to understand if the two mechanisms have evolved from each other and which was the first (Nieuwburg et al. 2021). From the data, it can be assumed, but much more information is needed, that the mechanisms also depend on the sociality of the studied species, on their habitat, and on the type of studied signal (visual or auditory) and that therefore a certain answer cannot be given; we could hypothesize by observing cases of autonomous and parallel evolution of these capacities (Nieuwburg et al. 2021). However, we can certainly say that many non-human species belonging to the order of primates possess these skills in more or less sophisticated forms

and that they all share a brain organized in a very similar way, with comparable scale laws, with a very dense neuron packed cerebellum connected to many different brain cortex areas capable of supporting new complex visual-motor and social behaviors (Nieuwburg et al. 2021).

A lot of studies (Ferretti and Papaleo 2019) have shown that many social mammals (dogs, horses, primates, sheep) possess skills related to the recognition of emotions (emotional contagion, contagious yawning, scratching, mimicry, consolation behavior, adaptive behavioral responses to signal like eyes opening, ears moving, lip-smacking, facial expressions) and that these abilities can be extended to recognize emotions also between different species (interspecies interactions). Attempts are being made to expand this type of study to other animals, such as invertebrates (Perry and Baciadonna 2017). There remain many difficulties in approaching the study of emotions in this kind of creatures; above all the *Aplysia*, the *Drosophila*, and the bees have been studied (the latter with complex collective and social behaviors). There have been observed variations related to ingeniously crafted stimuli that can be linked to fear and with optimistic and pessimistic behaviors (Perry and Baciadonna 2017). Also, if even in brains as simple as those of the invertebrates described above, phenomena that can be compared to emotional processing can be recognized, it is practically impossible to compare them to the behaviors and abilities observed in social mammals. This observation would be very interesting given the absence of a structure like the cerebellum in these invertebrates under study. However, it is interesting to note that in more complex invertebrates such as the octopus which, from the point of view of ethological observation, demonstrate very complex and behaviors suggestive of emotional processing (Crook 2021), the cerebellum is not present as in the social mammals described above. Even more interesting, however, is the comparative study of the brain structures of cephalopods which identified brain structures with a cellular organization like that of the cerebellum (Shigeno et al. 2018). We generally speak of convergent

evolution. Whether this structure can also be involved in the production and recognition of emotions is certainly not possible to say now, but it is an interesting idea that would deserve to be explored.

4.3 Evidence of Cerebellum Involvement in Social Cognition

In 100 milliseconds, humans can decode many social cues that inform about the emotional state of others guiding their behavior. This skill is part of social cognition, the capacity used by humans to understand and interact with other people in a social environment (Frith and Frith 2012). The ability to recognize emotive facial expressions is one of its most important features. The perception of others as subjects endowed with goals, beliefs, thoughts, and emotions, as well as the use of these talents to establish interactions between two or more individuals, will be included in the basic competencies of social cognition (e.g., attachment, teamwork, obedience, imitation, respect of social norms). Children can respond to social stimuli (e.g., facial expressions, joint attention) at a very early stage in their development (Richards 1974; Striano and Reid 2006), and developing these abilities is critical. However, there are numerous unanswered problems, the most important of which is whether social cognition is a distinct type of cognition or if it is based on a general mechanism adapted from emotion and cognitive processing. It is important to note that the cerebellum is engaged in many cognitive and affective skills that are required for good social cognition functioning, but its specificity is more debatable. Two main topics in social cognition recall the two main mechanisms of emotion recognition: the mirroring field, and the theory of mind (ToM) field, which studies the role of mid-line structures in mentalizing about the states of others (Keysers and Gazzola 2007). The study of important brain areas for social cognition has revealed that it requires a large, distributed network that connects many different areas specialized in different tasks, such as goal

selection, action planning, appraisal, and evaluation, rather than a single specialized area with a small number of neurons (Adolphs 2009). An important specialized area, for humans, is the fusiform gyrus and, in general, the lower ventral areas of the temporal lobe that are important for semantic decoding of shapes and the visual processing of faces (Fonville et al. 2014; Harry et al. 2013). However, it has been shown that other areas are involved when expressions become dynamic and are not simple static images; in this case, the inferior occipital gyrus and the superior temporal sulcus play a decisive role working together (Ishai 2008). Premotor areas, in particular the ventral area F5 which contains mirror neurons in monkeys, were observed to be active in the perception of expressions (Likowski et al. 2012). Another key area for the recognition of emotions is the amygdala (Adolphs 2010). Many have hypothesized that there are two different processing paths, a fast and phylogenetically older one aimed above all at the recognition of fear that includes the amygdala and a slower one capable of greater detail and precision in the classification (Dolan and Vuilleumier 2003). It is not clear whether the fast path is somehow independent of consciousness or if there are simply parallel channels involving multiple areas including, among others, the amygdala, the orbitofrontal cortex, the anterior insula, and the anterior cingulate cortex (Pessoa et al. 2002). Furthermore, the idea that the amygdala can only be involved in the recognition of fear, or general negative emotions related to avoidance behaviors, has recently been challenged. Currently, the opinion is that the amygdala can rapidly discriminate the emotional value and therefore also process positive emotions (Britton et al. 2006). It is very interesting to note that the cerebellum plays a significant role in this network by working together with many of the aforementioned areas. Depending on the brain area, there are specific connections to the cerebellum that can work together with integration and automation functions. It is therefore certain that the cerebellum relates to this network, less certain its role. In particular, the posterior lateral cerebellum (Crux I and II) works together with the prefrontal

cortices, while the posterior cerebellar vermis works together with the amygdala and the ventral orbitofrontal medial areas (Adamaszek et al. 2017).

Some studies, especially in the rat, have tried to clarify which areas are responsible for emotion-based behaviors and have found some overlap between the different species. The amygdala, the insula, and the anterior cingulate cortex were found as significant areas (Ferretti and Papaleo 2019). However, the precise role that these areas play in emotional recognition in animals remains to be clarified.

However, also if we can describe the network related to social cognition, it remains to be demonstrated if social cognition is hard-wired into the brain or not (Baetens et al. 2014; Balsters et al. 2013). There is convincing evidence derived from data obtained in healthy subjects and patients with cerebellar damage of the involvement of the cerebellum in many basic social cognition skills. Healthy subjects showed posterior cerebellar activations during joint attention (Gordon et al. 2013), during anticipation of social group success (Aue 2014), during observation and imitation of facial emotions (especially negative emotions), during goal-directed actions (Gazzola and Keysers 2009; Schraa-Tam et al. 2012), and during mother–infant interaction (Rocchetti et al. 2014). In a meta-analysis (Van Overwalle et al. 2014), partial involvement of the cerebellum was found in event or person mentalizing or mirroring tasks. In addition, a critical contribution to higher abstraction mentalizing was found as well. Several important findings correlate connections of the cerebellum to brain areas, in particular, the amygdala and the frontal cortex, with the size of the social group or social status, both in humans (Kanai et al. 2012; Zink et al. 2008) and in monkeys (Noonan et al. 2014; Sallet et al. 2011).

Cerebellar stroke patients showed impairment in the ability to recognize emotions (Adamaszek et al. 2014, 2015). In the first study, Tübingen Affect Battery (TAB) was used to assess recognition of emotional facial expression and emotional prosody in 15 patients with a cerebellar infarction and 10 age-matched controls. The patient group

revealed only slight to moderate ataxia or dysarthria, and no disturbances of ocular movement or evidence of mood disorder. There was no significant difference between groups in simple discrimination subtests, but the patient group had lower performance than controls in emotional subtests. The amount of impairment was greater for more demanding tasks such as cognitive and cross-modal subtests, as evidenced by large effect sizes. This pattern of impairment was observed for both facial and prosody stimuli. In patients, fear was significantly associated with more errors; the larger the volume of the lesion the greater the deficit on more emotional and complex tasks. The great majority of the patient sample had lesions of the posterior lobes of the cerebellum (see Fig. 1, first row). The second study comprised eight patients with discrete ischemic cerebellar lesions and eight control patients without any cerebrovascular stroke using event-related potential (ERP) to measure responses to faces from the Karolinska Directed Emotional Faces Database. Analyzing the late ERP responses, the N170 amplitude, indexing early perception of faces, was pronounced in all participants for faces compared to non-face neutral images indicating preserved recognition of faces in comparison to non-facial stimuli for both samples. Also, the late positive potential (LPP) showed clear augmentation to faces compared to non-facial neutral stimuli in both groups, but late ERP in parietal areas responses to emotional vs. neutral face expressions, however, was only significantly increased for faces with an emotional expression compared to neutral faces in the control group. Analyzing each facial emotional expression, the cerebellar lesion group showed diminished LPP for anger and particularly for fear (the other emotions showed only a trend), a negative correlation between the volume of cerebellar infarction and LPP for fear at both parietal sensors, and a strong negative correlation between some TAB subtests and diminished LPP for fear. Correlation analysis indicated that lesions of cerebellar area Crus I contribute to ERP deviations (see Fig. 1, third row, for the localization of the lesions).

Similar results have been found in patients with cerebellum degeneration (spinocerebellar

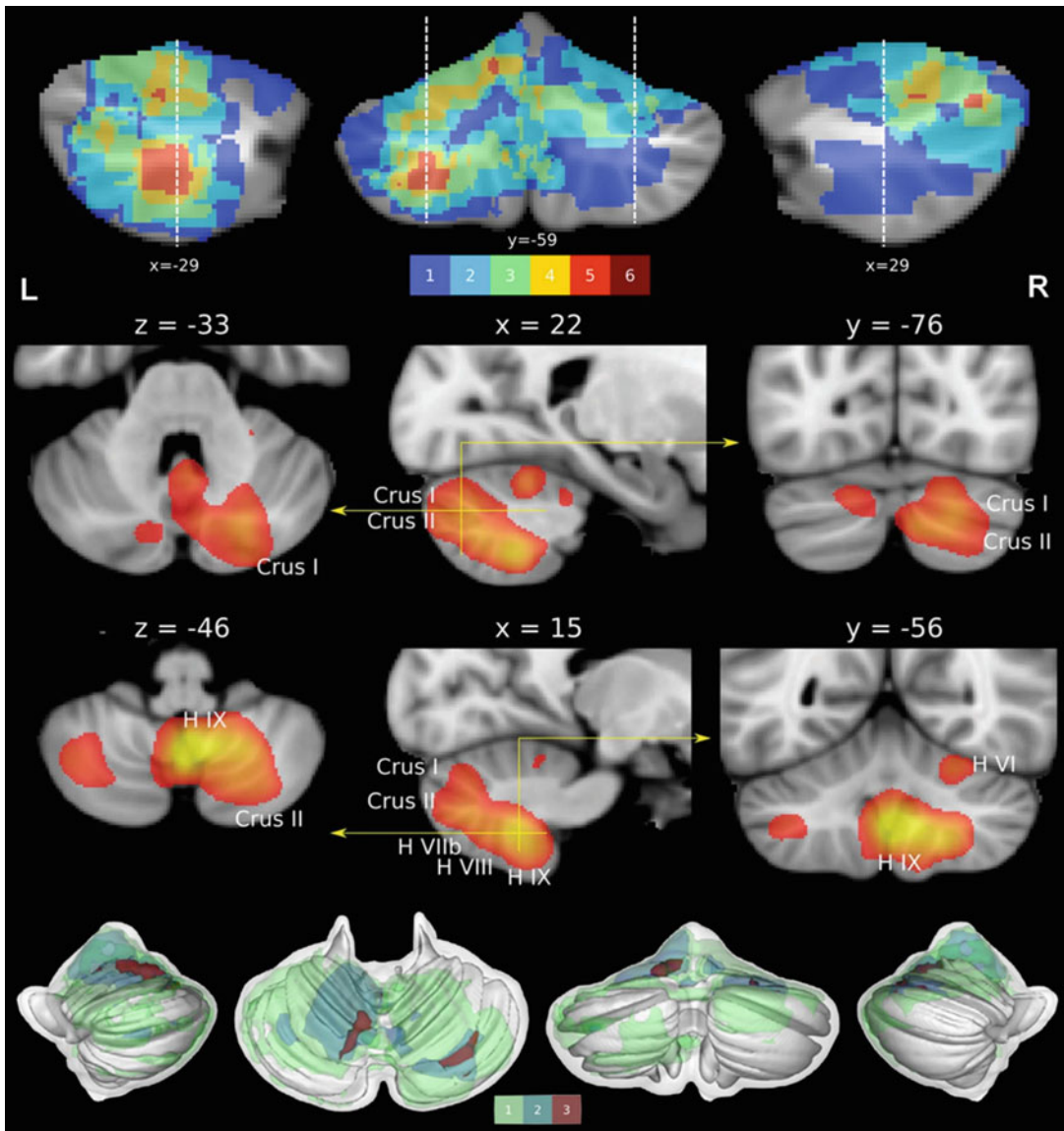


Fig. 1 Lesion mapping correlations for stroke and deficits in emotion recognition. *L* left, *R* right, *H* cerebellar hemisphere, MNI coordinates in mm. Composite image of cerebellar lesions of patient sample superimposed on axial, coronal, and sagittal projections of the cerebellum.

First row 15, second row 22, and third row 8 stroke patients. The overlapping is color coded (second row red = 1 patient, yellow = 3 patients). Adapted by Adamaszek et al. (2014, 2015, 2019) with permission

ataxia); they had deficits in ToM and recognition of face emotional expressions, especially of social emotions like guilt, with a gradient related to the complexity of the stimulus (Clausi et al. 2018; D'Agata et al. 2011; Sokolovsky et al. 2010). The specificity of these findings can be questioned;

cerebellar degeneration could be large nonfocal and associated with psychological and neuropsychological dysfunctions (Orsi et al. 2011). Also, cerebellar strokes could be associated with a wide spectrum of psychological, behavioral, and cognitive alterations (Adamaszek et al. 2017).

Two studies strengthened the link between cerebellum and emotion recognition beyond a simple correlation. In the first (Adamaszek et al. 2019) the controls to compare the 22 cerebellar strokes (CI) were 22 Parkinson's disease patients (PD) and 16 supratentorial strokes. In the study also age, cognition, and mood were controlled to mitigate the confounding factors. There were no differences for age, sex, education, or handedness between the 3 groups; low BARS scores indicated motor disabilities below the moderate level; thus, patients predominately had slight to moderate ataxia or dysarthria, section III UPDRS scores indicated moderate motor impairment for PD, and supratentorial stroke subjects had only slight motor disability with a low NIHSS score. On post hoc testing, CI was significantly lower, attributable to the TAB emotional subtests, but not the perception subtests. In CI fear errors were significantly greater. Examining topographic descriptors, the most common lesions were in the posterior cerebellum (crus 1, crus 2, or both) and the 3 patients without involvement of these regions had normal TAB scores (see Fig. 1, second row). The neuropsychological assessment did not reveal significant differences between the groups.

In the second (Ferrucci et al. 2012) 22 right-handed volunteers participated in the study; reaction times (RTs) and accuracy (number of incorrect responses) were collected during an emotion recognition task. Anodal and cathodal cerebellar tDCS (20 minutes) both significantly enhanced sensory processing in response to negative facial expressions but left positive emotion and neutral facial expressions unchanged. Sham tDCS and over the right prefrontal cortex did not have any effect.

Patients with schizophrenia have changes in fronto-temporal-thalamo-cerebellar networks, decreased cerebellum volume, and cerebellar neurotransmitter dysfunctions in clinical groups (Yeganeh-Doost et al. 2011). Affective bluntness, emotion detection deficiencies, and social difficulties are all hallmarks of schizophrenia, and they may be linked to cerebellar-derived changes in emotion, leading to conflicting findings for ToM (Mothersill et al. 2016).

Research on autism spectrum disorder provides some of the most convincing evidence (ASD). The deletion of *Tsc1* (tuberous sclerosis 1) produces morphological changes in Purkinje cells as well as aberrant behavior, including disrupted social interactions, in genetically engineered mice, implying a direct relationship between cell function and ASD deficits (Tsai et al. 2012). Patterns of ASD gene coexpression are specifically expressed in the cerebellum throughout the early postnatal years; also, early disturbance of the cerebellar circuitry is strongly connected with ASD, with a risk ratio as high as 40 (Wang et al. 2014).

Developmental diaschisis is a fundamental concept that has emerged: cerebellar dysfunction during critical sensitive periods may disrupt the maturation of distant neocortical circuits (Wang et al. 2014); ASD deficits resulting from early-life lesions are, with the exception of the cerebellum, to a large extent recoverable over time (Fig. 2).

Many ASD symptoms (motor, emotional, and social) can be grouped into a framework that shows the illness as a prediction deficit (Sinha et al. 2014) caused by a loss of frontal cortex-cerebellum connectivity throughout development.

This fronto-cerebellar network may play a role in both ontogeny and phylogeny. It has been discovered that the posterior cerebellar lobes, frontal cortices, and pontine connections coevolved in parallel in monkeys and humans (Balsters et al. 2010; Ramnani et al. 2006). These cerebello-thalamo-cortical networks are important in human evolution (Barton 2012), but whether the use of tools or the size and complexity of the social group was the key determinant of evolutionary pressure is still debated (Dunbar and Shultz 2007). Some researchers used phylogenetic comparative analysis to show that the cerebellum and frontal structures not only co-evolved but were also related to tool development and the size of the social group (Barton 2012). This means that if we think of the cerebellum as part of a single system, both in terms of phylogeny and ontogeny, we can see how vital it is in the development of many critical social cognitive skills.

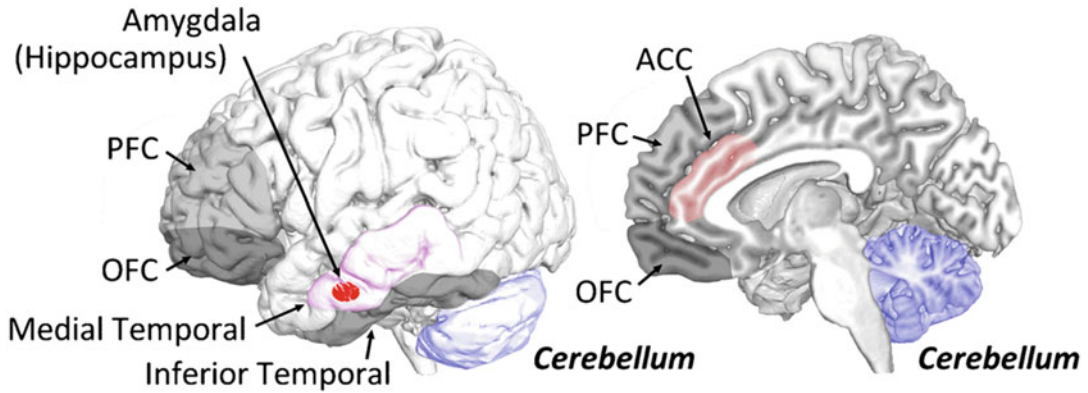


Fig. 2 Lesion mapping for early and late injuries resulting in autism social deficits. Brain areas result in lasting autism spectrum disorders and social deficits when injured neonatally (blue), in adulthood (red), or that can be fully or partially compensated after an injury regardless of age (light or dark gray). Medial temporal area is depicted in violet to indicate that both neonatal and adult injuries can cause social deficits, but only if the whole medial structures are damaged; for neonatal lesions, deficits are

not compensable. Data about ACC neonatal lesion are nowadays lacking. *PFC* prefrontal cortex, *ACC* anterior cingulate cortex, *OFC* orbitofrontal cortex. Brain renders were realized with Mango (<http://ric.uthscsa.edu/mango>) from the MRIcron canonical ch2better.nii template (<http://www.mccauslandcenter.sc.edu/mricron/mricron>). Adapted by (Wang et al. 2014). Copyright 2014 by Cell Press. Adapted with permission

4.4 Conclusions and Future Research

In conclusion, we can summarize the chapter.

First, in the future, it is necessary to improve the definition of emotion to make the experimental results more comparable. However, since this is a problematic and complex operation, researchers should, at least, start by clearly signaling their position, making explicit the operational definition of the measures used and the theoretical framework adopted.

Second, we can affirm, with some confidence, that there is evidence of the involvement of the cerebellar system in emotion. Similarly, we can consider as probable the role of the cerebellum in social cognition in understanding the emotional state of other humans, especially when they express negative emotions such as fear. However, doubts remain about the specificity and the moment in which this role is played. It is therefore essential to investigate with causal studies and no longer just correlational ones. A family of techniques that appears very promising in this sense is that of noninvasive brain

neurostimulation (NIBS). For such studies to be valid they must be properly constructed. A suggestion could be to start from the coordinates extracted from meta-analyses of neuroimaging studies to hypothesize the cerebellar areas most likely involved and to use these as neurostimulation targets. A paradigm of interference during emotional recognition tasks seems to be the first choice, ideally repeating the interference at different times, guided by an accurate timing that can distinguish the various stages of processing during emotional recognition, perhaps using EEG monitoring, compatible with the stimulation for triggering. Furthermore, an adequate number of multiple control conditions must be considered to reinforce the conclusions. It should be verified that stimulations of the frontal cortex do not lead to the same type of interference and that stimulations on the back of the head, close to the scalp coordinates of cerebellar stimulation but affecting the visual occipital cortex, do not have a similar effect. Finally, cognitive and attentional tasks should also be evaluated during stimulation of the same cerebellar and control sites of

stimulation to verify the cerebellum specificity during emotional processing.

References

- Adamaszek M, D'Agata F, Kirkby KC, Trenner MU, Sehm B, Steele CJ, Berneiser J, Strecker K (2014) Impairment of emotional facial expression and prosody discrimination due to ischemic cerebellar lesions. *Cerebellum* (London, England) 13(3):338–345. <https://doi.org/10.1007/s12311-013-0537-0>
- Adamaszek M, Kirkby KC, D'Agata F, Olbrich S, Langner S, Steele C, Sehm B, Busse S, Kessler C, Hamm A (2015) Neural correlates of impaired emotional face recognition in cerebellar lesions. *Brain Res* 1613:1–12. <https://doi.org/10.1016/j.brainres.2015.01.027>
- Adamaszek M, D'Agata F, Ferrucci R, Habas C, Keulen S, Kirkby KC, Leggio M, Mariën P, Molinari M, Moulton E, Orsi L, Van Overwalle F, Papadelis C, Priori A, Sacchetti B, Schutter DJ, Styliadis C, Verhoeven J (2017) Consensus paper: cerebellum and emotion. *Cerebellum* (London, England) 16(2):552–576. <https://doi.org/10.1007/s12311-016-0815-8>
- Adamaszek M, D'Agata F, Steele CJ, Sehm B, Schoppe C, Strecker K, Woldag H, Hummelsheim H, Kirkby KC (2019) Comparison of visual and auditory emotion recognition in patients with cerebellar and Parkinson's disease. *Soc Neurosci* 14(2):195–207. <https://doi.org/10.1080/17470919.2018.1434089>
- Adolphs R (2009) The social brain: neural basis of social knowledge. *Annu Rev Psychol* 60:693–716. <https://doi.org/10.1146/annurev.psych.60.110707.163514>
- Adolphs R (2010) What does the amygdala contribute to social cognition? *Ann N Y Acad Sci* 1191(1):42–61. <https://doi.org/10.1111/j.1749-6632.2010.05445.x>
- Aristotle (1987) *La Poetica: Testo greco a fronte*. Rizzoli, Milan
- Aristotle (2014) *Retorica: Testo greco a fronte*. Bompiani, Milan
- Aue T (2014) I feel good whether my friends win or my foes lose: brain mechanisms underlying feeling similarity. *Neuropsychologia* 60:159–167. <https://doi.org/10.1016/j.neuropsychologia.2014.05.025>
- Baetens K, Ma N, Steen J, Van Overwalle F (2014) Involvement of the mentalizing network in social and non-social high construal. *Soc Cogn Affect Neurosci* 9(6):817–824. <https://doi.org/10.1093/scan/nst048>
- Balsters JH, Cussans E, Diedrichsen J, Phillips KA, Preuss TM, Rilling JK, 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>
- Balsters JH, Whelan CD, Robertson IH, Ramnani N (2013) Cerebellum and cognition: evidence for the encoding of higher order rules. *Cereb Cortex* 23(6):1433–1443. <https://doi.org/10.1093/cercor/bhs127>
- Barrett LF, Adolphs R, Marsella S, Martinez AM, Pollak SD (2019) Emotional expressions reconsidered: challenges to inferring emotion from human facial movements. *Psychol Sci Public Interest* 20(1):1–68. <https://doi.org/10.1177/1529100619832930>
- Barton RA (2012) Embodied cognitive evolution and the cerebellum. *Philos Trans R Soc B Biol Sci* 367(1599):2097–2107. <https://doi.org/10.1098/rstb.2012.0112>
- Bracha V, Zhao L, Irwin KB, Bloedel JR (2000) The human cerebellum and associative learning: dissociation between the acquisition, retention and extinction of conditioned eyeblinks. *Brain Res* 860(1–2):87–94. [https://doi.org/10.1016/S0006-8993\(00\)01995-8](https://doi.org/10.1016/S0006-8993(00)01995-8)
- Britton JC, Phan KL, Taylor SF, Welsh RC, Berridge KC, Liberzon I (2006) Neural correlates of social and non-social emotions: an fMRI study. *NeuroImage* 31(1):397–409. <https://doi.org/10.1016/j.neuroimage.2005.11.027>
- Clausi S, Olivito G, Lupo M, Siciliano L, Bozzali M, Leggio M (2018) The cerebellar predictions for social interactions: theory of mind abilities in patients with degenerative cerebellar atrophy. *Front Cell Neurosci* 12:510. <https://doi.org/10.3389/fncel.2018.00510>
- Crook RJ (2021) Behavioral and neurophysiological evidence suggests affective pain experience in octopus. *IScience* 24(3):102229. <https://doi.org/10.1016/j.isci.2021.102229>
- Cuff BMP, Brown SJ, Taylor L, Howat DJ (2016) Empathy: a review of the concept. *Emot Rev* 8(2):144–153. <https://doi.org/10.1177/1754073914558466>
- D'Agata F, Caroppo P, Baudino B, Caglio M, Croce M, Bergui M, Tamietto M, Mortara P, Orsi L (2011) The recognition of facial emotions in spinocerebellar ataxia patients. *Cerebellum* 10(3):600–610. <https://doi.org/10.1007/s12311-011-0276-z>
- Damasio AR (1994) *Descartes' error: emotion, reason, and the human brain*. Putnam, New York
- Darwin C, Ekman P (coll.) (2009) *The expression of the emotions in man and animals* (4th ed., 200th anniversary ed). Oxford University Press, Oxford
- Descartes R (2011) *Meditazioni metafisiche*. Laterza, Bari
- Descartes R (2010) *Le passioni dell'anima*. Bompiani, Milan
- Dolan RJ, Vuilleumier P (2003) Amygdala automaticity in emotional processing. *Ann N Y Acad Sci* 985:348–355. <https://doi.org/10.1111/j.1749-6632.2003.tb07093.x>
- Dunbar RIM, Shultz S (2007) Evolution in the social brain. *Science* 317(5843):1344–1347. <https://doi.org/10.1126/science.1145463>
- Ekman P (2009) Darwin's contributions to our understanding of emotional expressions. *Philos Trans R Soc B Biol Sci* 364(1535):3449–3451. <https://doi.org/10.1098/rstb.2009.0189>
- Errante A, Fogassi L (2020) Activation of cerebellum and basal ganglia during the observation and execution of

- manipulative actions. *Sci Rep* 10(1):12008. <https://doi.org/10.1038/s41598-020-68928-w>
- Ferretti V, Papaleo F (2019) Understanding others: emotion recognition in humans and other animals. *Genes Brain Behav* 18(1):e12544. <https://doi.org/10.1111/gbb.12544>
- Ferrucci R, Giannicola G, Rosa M, Fumagalli M, Boggio PS, 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. *Cognit Emot* 26(5):786–799. <https://doi.org/10.1080/02699931.2011.619520>
- Fonville L, Giampietro V, Surguladze S, Williams S, Tchanturia K (2014) Increased BOLD signal in the fusiform gyrus during implicit emotion processing in anorexia nervosa. *Neuroimage Clin* 4:266–273. <https://doi.org/10.1016/j.nicl.2013.12.002>
- Frith CD, Frith U (2012) Mechanisms of social cognition. *Annu Rev Psychol* 63(1):287–313. <https://doi.org/10.1146/annurev-psych-120710-100449>
- Gazzola V, Keysers C (2009) The observation and execution of actions share motor and somatosensory voxels in all tested subjects: single-subject analyses of unsmoothed fMRI data. *Cereb Cortex* 19(6):1239–1255. <https://doi.org/10.1093/cercor/bhn181>
- Gordon I, Eilbott JA, Feldman R, Pelphrey KA, Vander Wyk BC (2013) Social, reward, and attention brain networks are involved when online bids for joint attention are met with congruent versus incongruent responses. *Soc Neurosci* 8(6):544–554. <https://doi.org/10.1080/17470919.2013.832374>
- Harry B, Williams MA, Davis C, Kim J (2013) Emotional expressions evoke a differential response in the fusiform face area. *Front Hum Neurosci* 7:692. <https://doi.org/10.3389/fnhum.2013.00692>
- Hume D (1987) *Opere filosofiche*. Laterza, Rome
- Ishai A (2008) Let's face it: It's a cortical network. *NeuroImage* 40(2):415–419. <https://doi.org/10.1016/j.neuroimage.2007.10.040>
- Kanai R, Bahrami B, Roylance R, Rees G (2012) Online social network size is reflected in human brain structure. *Proc R Soc B Biol Sci* 279(1732):1327–1334. <https://doi.org/10.1098/rspb.2011.1959>
- Keysers C, Gazzola V (2007) Integrating simulation and theory of mind: from self to social cognition. *Trends Cogn Sci* 11(5):194–196. <https://doi.org/10.1016/j.tics.2007.02.002>
- Kozioł LF, 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, Vandervort 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>
- Likowski KU, Mühlberger A, Gerdes ABM, Wieser MJ, Pauli P, Weyers P (2012) Facial mimicry and the mirror neuron system: simultaneous acquisition of facial electromyography and functional magnetic resonance imaging. *Front Hum Neurosci* 6:214. <https://doi.org/10.3389/fnhum.2012.00214>
- Lucretius Carus T (2013) *De rerum natura*. UTET Turin
- Mothersill O, Knee-Zaska C, Donohoe G (2016) Emotion and theory of mind in schizophrenia—investigating the role of the cerebellum. *Cerebellum* 15(3):357–368. <https://doi.org/10.1007/s12311-015-0696-2>
- Nieuwburg EGL, Ploeger A, Kret ME (2021) Emotion recognition in nonhuman primates: how experimental research can contribute to a better understanding of underlying mechanisms. *Neurosci Biobehav Rev* 123:24–47. <https://doi.org/10.1016/j.neubiorev.2020.11.029>
- Noonan MP, Sallet J, Mars RB, Neubert FX, O'Reilly JX, Andersson JL, Mitchell AS, Bell AH, Miller KL, Rushworth MFS (2014) A neural circuit Covarying with social hierarchy in macaques. *PLoS Biol* 12(9):e1001940. <https://doi.org/10.1371/journal.pbio.1001940>
- Orsi L, D'Agata F, Caroppo P, Franco A, Caglio MM, Avidano F, Manzone C, Mortara P (2011) Neuropsychological picture of 33 spinocerebellar ataxia cases. *J Clin Exp Neuropsychol* 33(3):315–325. <https://doi.org/10.1080/13803395.2010.518139>
- Perry CJ, Baciadonna L (2017) Studying emotion in invertebrates: what has been done, what can be measured and what they can provide. *J Exp Biol* 220(21):3856–3868. <https://doi.org/10.1242/jeb.151308>
- Pessoa L, McKenna M, Gutierrez E, Ungerleider LG (2002) Neural processing of emotional faces requires attention. *Proc Natl Acad Sci U S A* 99(17):11458–11463. <https://doi.org/10.1073/pnas.172403899>
- Ramnani N, Behrens TEJ, Johansen-Berg H, Richter MC, Pinsk MA, Andersson JLR, Rudebeck P, Ciccarelli O, Richter W, Thompson AJ, Gross CG, Robson MD, Kastner S, Matthews PM (2006) The evolution of prefrontal inputs to the Cortico-pontine system: diffusion imaging evidence from macaque monkeys and humans. *Cereb Cortex* 16(6):811–818. <https://doi.org/10.1093/cercor/bhj024>
- Richards M (1974) *The integration of a child into a social world*. Cambridge University Press, Cambridge
- Rocchetti M, Radua J, Paloyelis Y, Xenaki L, Frascarelli M, Caverzasi E, Politi P, Fusar-Poli P (2014) Neurofunctional maps of the 'maternal brain' and the effects of oxytocin: a multimodal voxel-based meta-analysis. *Psychiatry Clin Neurosci* 68(10):733–751. <https://doi.org/10.1111/pcn.12185>
- Sallet J, Mars RB, Noonan MP, Andersson JL, O'Reilly JX, Jbabdi S, Crosson PL, Jenkinson M, Miller KL, Rushworth MFS (2011) Social network size affects neural circuits in macaques. *Science* 334(6056):697–700. <https://doi.org/10.1126/science.1210027>
- Sartre J-P, Pirillo N (2004) *L'immaginazione; Idee per una teoria delle emozioni*. Bompiani, Milan
- Scarantino A, de Sousa R (2021) Emotion. In Zalta EN (ed.), *The Stanford encyclopedia of philosophy*

- (summer 2021). Metaphysics Research Lab, Stanford University. <https://plato.stanford.edu/archives/sum2021/entries/emotion/>
- Schraa-Tam CKL, Rietdijk WJR, Verbeke WJMI, Dietvorst RC, van den Berg WE, Bagozzi RP, De Zeeuw CI (2012) fMRI activities in the emotional cerebellum: a preference for negative stimuli and goal-directed behavior. *Cerebellum* (London, England) 11(1):233–245. <https://doi.org/10.1007/s12311-011-0301-2>
- Shigeno S, Andrews PLR, Ponte G, Fiorito G (2018) Cephalopod brains: an overview of current knowledge to facilitate comparison with vertebrates. *Front Physiol* 9:952. <https://doi.org/10.3389/fphys.2018.00952>
- Sinha P, Kjelgaard MM, Gandhi TK, Tsourides K, Cardinaux AL, Pantazis D, Diamond SP, Held RM (2014) Autism as a disorder of prediction. *Proc Natl Acad Sci* 111(42):15220–15225. <https://doi.org/10.1073/pnas.1416797111>
- Sokolovsky N, Cook A, Hunt H, Giunti P, Cipolotti L (2010) A preliminary characterisation of cognition and social cognition in spinocerebellar ataxia types 2, 1, and 7. *Behav Neurol* 23(1–2):17–29. <https://doi.org/10.1155/2010/395045>
- Spinoza B (2017) *Etica*. Bompiani, Milan
- Striano T, Reid VM (2006) Social cognition in the first year. *Trends Cogn Sci* 10(10):471–476. <https://doi.org/10.1016/j.tics.2006.08.006>
- Tsai PT, Hull C, Chu Y, Greene-Colozzi E, Sadowski AR, Leech JM, Steinberg J, Crawley JN, Regehr WG, Sahin M (2012) Autistic-like behaviour and cerebellar dysfunction in Purkinje cell Tsc1 mutant mice. *Nature* 488(7413):647–651. <https://doi.org/10.1038/nature11310>
- 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>
- Wang SS-H, Kloth AD, Badura A (2014) The cerebellum, sensitive periods, and autism. *Neuron* 83(3):518–532. <https://doi.org/10.1016/j.neuron.2014.07.016>
- Yeganeh-Doost P, Gruber O, Falkai P, Schmitt A (2011) The role of the cerebellum in schizophrenia: from cognition to molecular pathways. *Clinics* 66:71–77. <https://doi.org/10.1590/S1807-59322011001300009>
- Zink CF, Tong Y, Chen Q, Bassett DS, Stein JL, Meyer-Lindenberg A (2008) Know your place: neural processing of social hierarchy in humans. *Neuron* 58(2):273–283. <https://doi.org/10.1016/j.neuron.2008.01.025>