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# Cerebellum and Emotion Processing

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## Abstract

Clinical examinations and neuroimaging investigations have dramatically changed the prevailing view of human cerebellar function and suggest contributions beyond movement control. Of these new views, perhaps the most intriguing proposal is that the cerebellum plays a key role in regulating emotion. According to the *dysmetria of thought* theory, the cerebellum provides accuracy, consistency and appropriateness to cognitive and affective functions, as it does for movement-related operations. Despite the value of a universal theory on the cerebellar function, it is also essential to consider its unique contributions to specific functional domains. This chapter aims to provide an accentuated account of the cerebellar role in emotion processing by separately evaluating its impact for sub-components of emotion processing. These include physiological responses that contribute to the subjective or “feeling” component of emotion, emotional expressions that serve essential social-communicative functions, and the cognitive appraisal process that determines the emotional significance of events and therefore affects the generation and modulation of emotions.

## Cerebellum and Emotion Processing

The cerebellum has an important and well-known role in the control and coordination of movements. In 1824, Pierre Flourens, one of the founders of modern neuroscience, removed the entire cerebellum of a pig to investigate its functional role in behaviour. After the procedure, the pig was unable to stand or walk. He repeated the process with similar results in pigeons and dogs, and concluded that the cerebellum is responsible for movement control (Flourens, 1824). Flourens' assertion matched the predominant clinical picture of cerebellar disease, which was long understood to result in imprecise movement control (Holmes, 1917, 1939). These and related explanations of the role of the cerebellum seem to have satisfied most scholars and clinicians, and effectively ended debate on the topic for the next 150 years. More recently, careful clinical examinations and neuroimaging investigations have dramatically changed the prevailing view of human cerebellar function and suggested instead contributions beyond movement control (Baumann et al., 2015; Koziol et al., 2014; Mariën et al., 2014; Van Overwalle et al., 2020). Of these views, perhaps the most intriguing proposal is that the cerebellum plays a key role in regulating emotion (Adamaszek et al., 2017). In a longitudinal follow-up study of 20 patients with cerebellar lesions, Schmahmann and Sherman observed significant behavioural and affective changes, now commonly known as the "cerebellar-cognitive–affective syndrome" (Schmahmann, 2004). Following this work, a spectrum of emotional and behavioural deficits has been described in patients with both acquired and congenital cerebellar damage, ranging from apathy and indifference to aggressive behaviour (Hoche et al., 2018).

In addition, human neuroimaging studies have provided evidence for a cerebellar role in emotion processing in non-clinical samples (Adamaszek et al., 2017; see also chapter 6:

“Topography of Emotion in Cerebellum”). For instance, we used functional magnetic resonance imaging (fMRI) to identify neural activity patterns within the cerebellum in 30 healthy human volunteers as they categorised images that elicited each of the five primary emotions: joy, anger, disgust, fear and sadness (Baumann & Mattingley, 2012). We found that stimuli within each category resulted in distinct patterns of cerebellar activity. However, we also found localised regions of overlap in the activation patterns across pairs of emotions, implying shared neural networks. For instance, there was partial overlap in activations associated with fear and anger (paravermal lobules VI and Crus I), anger and disgust (vermal lobule IX), and joy and sadness (vermal lobule VIIIA). Our study was the first to show that the cerebellum represents the five primary emotions in functionally distinct subregions, mirroring to some extent the segregation of emotion processing seen in the neocortex (e.g. Phan et al. 2002). In addition, our study showed that all five emotions evoked activity in the cerebellar vermis and the intermediate parts of the cerebellar hemispheres (i.e., the paravermis), thus highlighting a critical role for the medial cerebellum in emotional processing. In line with our results, clinical studies have reported that the affective component of the cerebellar cognitive–affective syndrome is most notable when lesions involve the vermis and paravermis (Schmahmann & Sherman, 1998; Schahman et al., 2007).

Further support for a cerebellar role in emotional processes comes from anatomical and electrophysiological studies in cats and non-human primates, showing cerebellar projections to emotion-related areas of the brain, including the hypothalamus, amygdala, and basal ganglia as well as the neocortex and brainstem nuclei (Anand et al., 1959, Blatt, et al., 2013; Middleton and Strick, 2001, Schmahmann, 2001; Schutter & van Honk, 2005, Snider & Maiti, 1976).

Given the evidence for cerebellar involvement in emotion processing, it is natural to ask what specific role it plays. According to the *dysmetria of thought* theory (Schmahmann, 1991), the cerebellum provides accuracy, consistency and appropriateness to cognitive and affective functions, as it does for movement-related operations. Building on this idea, Schmahmann (1996) coined the term “universal cerebellar transform”, to capture the idea of a singular functional principle. This hypothesis is underpinned by the observation that, in contrast to the neocortex, cerebellar anatomical organisation and computational principles are relatively uniform. Its macrostructural uniformity, characterised by repeating corticonuclear micro-complexes<sup>1</sup> (Schmahmann, 2019), is contrasted by a rich heterogeneity of topographically arranged connections with the rest of the brain (Buckner et al., 2011; Habas et al., 2009; O'Reilly et al., 2010). The deficits that emerge following cerebellar lesions are therefore largely determined by the function of the cortical areas to which the damaged cerebellar region is connected. In terms of its uniform computational principles, the cerebellum provides fast and parallel processing of its diverse inputs, but produces minimal outputs (Ito, 2006). More specifically, each input received by the cerebellum is processed by around 10,000 granule cells, the outputs of which converge on a much smaller number of Purkinje cells (around 200,000 granule cells are connected with just one Purkinje cell). The Purkinje cells send their outputs to a small group of deep nuclear cells, which project their signals back to the cortex and other subcortical areas via the thalamus (Linas et al., 2004). Information processing in the cerebellum is swift, and signals are typically processed within a couple of milliseconds (Snider & Stowell, 1944). The cerebellum is therefore considered essential for all sensory and motoric tasks that require high (i.e., millisecond range) temporal precision

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<sup>1</sup> See De Zeeuw (2021) for a review on the subtleties and subclassifications of microzones and microcomplexes at the cellular level.

Baumann et al., 2015; Ivry & Keele, 1989)<sup>2</sup>. These functional and structural features have led to the hypothesis that the cerebellum is ideally suited for the rapid detection of internal and external stimulus patterns, and can rapidly generate outputs that provide predictive state estimates (i.e., internal models; Ito, 2008)). Importantly, while neocortical brain areas are also known to be involved in the formation of mental models of the world, the cerebellum plays a unique role due to its ability to rapidly process internal and external signals and to therefore provide feedforward models, in contrast to feedback models, which are naturally slower (Adamaszek et al., 2017; Baumann et al. 2015; Koziol et al. 2014; Nixon, 2003).

Cerebellar feedforward models allow for the generation of corrective signals that help to maintain optimal performance in highly time-critical responses (Adamaszek et al., 2017; Baumann et al., 2015; Koziol et al., 2014; Nixon, 2003), akin to an oscillation dampener optimising performance (Schahmann, 2019). On this view, the cerebellum is regarded as a support structure that does not control, but rather fine-tunes cognitive and affective responses, akin to its role in motor behaviour.

Despite the value of a universal theory on the cerebellar function, it is also essential to consider its unique contributions to specific functional domains. This chapter aims to provide an accentuated account of the cerebellar role in emotion processing by separately evaluating its impact for sub-components of emotion processing. Emotions can be regarded as a multifactorial concept that includes *physiological* components (and subjective experience thereof) , *expressive* components, and *cognitive* components (Izard, 2010). In the following,

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<sup>2</sup> The timing hypothesis suggests that the cerebellum provides a near-infinite set of interval type timers, which allow for task-specific timing-functions (Bares, et al., 2019; Ivry 1997).

we will discuss the cerebellar contributions to each of these components before providing an integrative discussion and an outlook for research and practice.

### **Cerebellar contribution to the physiological component of emotion**

Physiological arousal has long been recognised as a key component of emotion (Lange, 1885; James, 1894; Schachter & Singer, 1962), and the cerebellum maintains projections to brain areas underpinning control of physiological arousal. Briefly, the autonomous nervous system, which is divided into sympathetic and parasympathetic branches, controls emotional arousal. The sympathetic branch is related to increased arousal and the functional role of preparing the body for action (“fight or flight”). In contrast, the parasympathetic system is related to decreased arousal and restorative body functions, such as sleep and digestion. Relative dominance of sympathetic vs. parasympathetic activation is associated with elevated responses in prominent markers of physiological arousal, such as heart rate, respiration and sweating response. In addition, there are some more subtle signals, such as changes in temperature, muscle tension and gastric activity (Levenson et al., 1990; Vianna & Tranel, 2006). The complex neural systems that underpin arousal are located in the brainstem, thalamus, hypothalamus and basal forebrain (Jones, 2003). These receive inputs from cortical and subcortical emotion processing areas including the amygdala, insula, basal ganglia and neocortex. The hypothalamus, in particular its paraventricular nucleus, plays a vital role in the modulation of arousal via its regulation of the pituitary gland and the secretion of hormones (Engelmann et al., 2004). Stimulation of the posterior hypothalamus has been found to modulate sympathetic arousal responses, such as pupillary dilatation, respiratory rate, heart rate and blood pressure (Hess, 1957).



Anatomical and electrophysiological studies in cats and non-human primates have shown direct cerebellar projections to crucial brain areas underpinning physiological arousal, including the hypothalamus (Blatt, et al., 2013). More specifically, the vermis, fastigial nucleus and interpositus nucleus maintain projections with key regions underlying the autonomous control of arousal (Strata, 2015). There is also direct functional evidence that implicates the cerebellum in modulating autonomic responses. Studies in cat have revealed that bilateral lesions of the rostral fastigial nucleus affect mean arterial pressure and reflexic heart rate responses, and lead to overall decreased resting heart rate (Chen et al., 1994). Similarly, a more recent study showed that microinjection of acetylcholine, and muscarinic acetylcholine receptor activation in the cerebellar cortex led to decreases in arterial pressure and heart rate (Zhang, et al. 2016). These outcomes suggest that the cerebellum augments sympathetic cardiovascular responses and inhibits parasympathetically mediated responses.

In humans, evidence for a cerebellar influence on autonomic arousal processes comes mainly from brain imaging studies. Styliadis and colleagues (2015) used magnetoencephalography to record the spatial and temporal profile of brain activity in response to emotion-evoking images. Importantly, Styliadis et al. (2015) investigated the distinct neural response to varying degrees of arousal and valence (i.e., the extent to which an emotion is positive vs. negative), using images from the International Affective Picture System (IAPS; Lang et al., 1999). The IAPS comes with normative ratings for stimuli along the orthogonal dimensions of arousal and valence. Overall, Styliadis et al. (2015) observed cerebellar responses ~160ms after stimulus onset. Using the arousal and valence ratings as regressors, they identified distinct areas of the cerebellum involved in the processing of those two affective dimensions. Specifically, whereas valence was related only to one hemispheric area of the cerebellum (left lobule VI), arousal was associated with activity in several vermal (lobule VI and VIIIa) and hemispheric areas (left

Crus II). The indication of a vermal role in modulating arousal is consistent with its anatomical connectivity profile, since it maintains direct bi-directional connections with the hypothalamus (Haines et al., 1984), as well as brainstem reticular nuclei (Brodal, 1975; Dietrichs & Walberg, 1979). These findings also align with our own fMRI data showing that the high-arousal emotions of fear and anger elicit activity in vermal lobule VI (Baumann & Mattingley, 2012). Apart from identifying this spatial pattern of emotional arousal vs. valence in the cerebellum, the study by Styliadis et al. (2015) also revealed new insights into the temporal domain of cerebellar processing. While valence-related activity appeared relatively late and was short-lived (420-530ms), arousal-related activity could be detected early and was sustained (160-980ms). These findings further support the notion that the cerebellum independently contributes to a physiological arousal component of emotion, as well as a cognitive component of emotion related to the appraisal of valence.

Physiological arousal is essential for bringing the body into a situation-appropriate state (i.e. fight/flight vs. restoration; Thayer, 1989). In addition, it is the conscious awareness of those bodily states, known as interoception, that leads to the subjective (“felt”) component of emotions (Critchley & Garfinkel, 2017). Nummenmaa and colleagues (2014) asked several hundred participants, using a topographical self-report tool, about the distinct bodily sensations they associate with specific emotions. The authors found that different emotional states (e.g. anger, sadness, joy) were associated with distinct, but culturally universal topographic somatotopic maps (i.e. the maps were consistent across Western European and Asian participants. For instance, whereas both anger and happiness were associated with perceived elevated activity in the upper chest (likely a reflection heart rate and respiration related changes), happiness, but not anger, also included sensations related to the gastric system. These observations are corroborated by human brain imaging studies showing

somatosensory activity correlated with emotion-related somatic experiences (Nummenmaa et al., 2012).

Given the diverse range of interoceptive channels and crosstalk between them, the neural systems underpinning such bodily sensations are complex. However, several lines of evidence indicate that the anterior insula is the central hub at which interoceptive signals converge, and the central structure underpinning subjective feelings (Craig, 2009; Strigo & Craig, 2016). Functional and structural MRI data have suggested that the size and activation of the anterior insula are related to individuals' ability and precision in detecting heartbeats (Critchley et al., 2004), and positron emission tomography data have shown that activity in the insula is related to gastric distensions (Barrett et al., 2004). Together these studies suggest that the insula underpins our ability to perceive internal bodily sensations and is crucial for the subjective feeling-related aspect of emotion. Importantly, human imaging studies have revealed functional connections between the insula and the cerebellum (Allen et al., 2005; Habas et al., 2009), suggesting a role of the cerebellum in interoceptive processing of arousal. In an fMRI study conducted by Gray and colleagues (2007), participants were presented with auditory signals that were either aligned or misaligned with their heartbeats. The condition that involved time-shifted auditory feedback led to increased activity in the insula and the cerebellar vermis (lobule VI), suggesting that both areas are involved in perceiving one's own heartbeat, i.e. interoception.

Finally, neuropsychological case studies of patients with isolated cerebellar lesions have provided compelling examples of dysregulated physiological arousal. For instance, Annoni and colleagues (2003) reported on a patient with left cerebellar stroke involving the fastigial nucleus who presented with undifferentiated skin conductivity responses to positive and

negative outcomes in a reinforcement learning task. These physiological abnormalities were further accompanied by blunted affect, highlighting the role of arousal in the modulation of emotion.

Taken together, the studies reviewed above provide compelling evidence that the cerebellum plays a central role in the modulation of autonomic physiological responses. As discussed, situation-appropriate states of arousal are not only important for bodily attitudes of action readiness, but also for consciously experienced feelings.

### **Cerebellar contribution to the expressive component of emotion**

While emotions help us, at the individual level, to avoid physical threats to our well-being, they also serve essential social-communicative functions (Keltner et al., 2006). For most people in stable, developed countries, threats to well-being are more likely to originate in the social rather than the physical environment. Emotions help us navigate social interactions and solve social problems by providing a communicative signal to those we interact with. Humans and other animals have potent nonverbal means to communicate emotional messages, including facial expressions, movement and posture signals, and vocal signals (Skinner, 2013). The display of emotional expressions can lead to specific, immediate and behavioural responses, highlighting the need for precise signalling to avoid miscommunication. In the facial expression of emotions, the movement of just a single muscle can significantly impact the perceived social message (Matsumoto & Hwang, 2014). For example, nuances in the expression of a smile might deflect or exacerbate hostile behaviour. Correspondingly, humans can recognise posed emotions with a high degree of certainty (McLellan et al., 2010). Moreover, the importance of precision in expressing emotions is highlighted by the problems experienced by individuals with dysregulated emotional functions.

Dysregulation of emotional expression can present in the form of exaggerated or blunted emotional expression. Interestingly, pathological expressions of emotion are often dissociated from the feeling component, e.g., exaggerated expressions of emotion are not necessarily linked to correspondingly exaggerated feelings (Poeck, 1985; see also chapter 18: “Cerebellum and Emotion Disorders”). As a post-stroke syndrome, dysregulation of emotion expression is most often seen after lesions involving the anterior cortex-internal capsule/basal ganglia-ventral brainstem circuitry (Kim & Choi-Kwon, 2000). The classic explanation for dysregulation of emotional expression is that it is caused by a lack of inhibition of subcortical nuclei that are in direct control of facial and respiratory function (Wilson, 1924). However, this loss-of-inhibition hypothesis is too simplistic to account for the clinical picture, because the dysregulation involves both increased and decreased intensity of emotional expressions, in addition to contextually inappropriate displays of emotion (Bharathi & Lee, 2006; Choi et al., 2013).

Cerebellar dysfunction has been proposed to explain the complex patterns of dysregulated expressions of emotions. Schmahmann and Sherman (1998) observed major behavioural and affective changes in patients with cerebellar damage, ranging from apathy to pathological crying and laughing. Further support for a cerebellar role in modulating emotional expressions comes from a case study by Parvizi and colleagues (2001), who reported on a patient who exhibited pathological crying and laughter post-stroke. This case is unique since the lesions were relatively small (in the millimetre range) and were confined to the white matter of the brainstem and cerebellum. These lesions were situated along white matter pathways connecting the cerebrum, brainstem and cerebellum. Thus, the patient’s symptoms were interpreted as being due to partial deafferentation of the cerebellum from descending cerebral inputs. The characteristics of the functional deficits, in combination with the specific

pattern of neural damage, supports the hypothesis that the cerebellum has a crucial role in maintaining emotional responses that are optimised in terms of intensity and timing (Adamaszek et al., 2017; Schahmann, 2019). The importance of temporal precision in facial expressions of emotion is well recognised, and evidenced by the fact that mental connotations can change within milliseconds (Ekman & Friesen, 1978; Haggard & Isaacs, 1966). The cerebellum exerts modulatory control over facial muscles via projections that originate in its dentate and interpositus nuclei, and that connect to the facial nuclei and brainstem via the red nucleus (Delgado-Garcia & Gruart, 2005; Gibson et al., 1987, Hoover & Strick, 1999; van Kan et al., 1993).

Likewise for vocal expressions of emotion, temporal precision is inherently important since carefully timed variations express the valence and intensity of an individual's emotions (Banziger & Scherer, 2005). Several reports have shown that the cerebellum plays an important regulatory role in vocal utterances (Mariën et al., 2014). The most well-known cause of vocal deficits after cerebellar damage is dysarthria, in which dysregulated control of the tongue and voice box leads to slurred speech. Dysarthria after cerebellar lesions is also associated with disordered phonation, which refers to inappropriate pitch or loudness of the sounds produced (Mariën et al., 2014). Neuroimaging studies have shown that speech production engages the representation of articulatory muscles in the sensorimotor cerebellum, specifically medial lobule VI bilaterally and the dentate nucleus (Thurling et al., 2011). In addition, data from human lesion studies suggest that the vermal and paravermal aspects of lobules V–VI and VII–VIII are involved in the production of vocal utterances (Mariën et al., 2014).

While emotional expressions can be consciously elicited and modulated, significant aspects of emotional expression and their detection are regulated automatically and thus apparently not under conscious control (de Gelder & Hadjikhani, 2006). The automatic and precise adjustment of emotional expressions based on incoming information requires the ability to predict state trajectories. There is a consensus that the cerebellum uses forward models to generate precise predictions of perceptual, sensorimotor and cognitive states (Adamaszek et al., 2017; Baumann et al., 2015; Koziol et al. 2014), which not only aid the generation of facial expressions but also their decoding by the perceiver. Emotion recognition deficits associated with transient disruption (via brain stimulation) or permanent cerebellar lesions have been reported for the visual (Ferrucci et al., 2012; Turner et al., 2007) as well as the auditory domain (Thomasson et al., 2019). Further evidence for a cerebellar role in implicit emotion processing comes from a repetitive transcranial magnetic stimulation (rTMS) study that showed that cerebellar stimulation, but not visual cortex stimulation, resulted in faster reaction times to subconsciously perceived (masked) images of happy faces (Schutter, et al., 2009).

### **Cerebellar contribution to the cognitive component of emotion**

While there are many definitions of cognition, in considering cognition as an integral component of emotion, it is useful to limit the definition to mental processes that depend on acquired representations (Izard, 1993; Izard & Malatesta, 1987). Those acquired mental representations of the physical and social environment are thought to allow for a dynamic appraisal process that can trigger and shape emotional states (Scherer, 1993). The cognitive appraisal process determines the emotional significance of events and therefore affects the generation and modulation of emotions. The appraisal process can be further

compartmentalised into several separate dimensions, such as the appraisal of goal-relevance, intentionality, and consistency with social norms (Ochsner & Gross, 2014; Scherer, 2001). In any given situation, multiple appraisals may coexist, resulting in multifaceted affective experiences and underlining the complexity of this process. The appraisal-related cognitive component of emotion is thought to exist on a continuum that ranges from simple and automatic discrimination to complex and deliberate appraisal processes (Izard, 1993; Izard & Malatesta, 1987). This conceptual continuum can be mapped onto a continuum of emotion-related brain systems, ranging from subcortical structures including the amygdala and striatum, to higher-level cortical systems such as the insula, orbitofrontal and ventromedial cortex (Damasio et al., 2000).

The prefrontal cortex is generally regarded as the prime cortical structure for regulating the more basic emotional processes originating in subcortical structures (Bechara & Damasio, 2005; Ochsner & Gross, 2014). The critical role of the prefrontal cortex in emotion regulation is evidenced by its involvement in almost all affective disorders (Dixon et al., 2017). According to the appraisal-by-content model, evaluation of the emotional significance of events serves as a unifying principle for the role of the prefrontal cortex in emotion processing (Dixon et al., 2017). Moreover, distinct subregions of the prefrontal cortex are specialised for supporting appraisals for different contexts and contents. The prefrontal-mediated cognitive appraisal process is therefore thought to lead to the generation of contextually appropriate emotions and action tendencies.

As for the other two components of emotion discussed above (i.e., physiology and expression), the cerebellum also plays a crucial role in the modulation of cognitive processes, resulting in improved and context-appropriate performance (Koziol et al., 2014). The fact that



the cerebellum is reciprocally connected with a range of limbic structures and prefrontal cortical areas provides a robust neuroanatomical argument in favour of cerebellar involvement in the cognitive component of emotion (Blatt et al., 2013; Middleton & Strick, 2001). Furthermore, behavioural evidence corroborates the idea of a cerebellar contribution to appraisal-related aspects of the generation and modulation of emotion. Van den Berg and colleagues (2020) compared the risk-taking attitudes of 134 patients with cerebellar lesions following stroke (involving the posterior lobes of the cerebellum, particularly in lobules VI, VIII, and Crus I) relative to a control group. Participants' risk-taking behaviour was assessed using the Action Selection Test (Vlakveld, 2011), which consists of driving scenarios and requires participants to indicate what they would do in a specific situation ("do nothing", "release accelerator", or "brake"). The main finding was that, compared with the control group, the cerebellar patients took significantly more risks. In addition, the same group of patients was impaired in recognising fearful expressions in the Ekman 60 Faces Test of the Facial Expressions of Emotions Battery (Young et al., 2002), which suggests that the impaired decision making behaviour is underpinned by deficits in emotion processing. While studies based on stroke-induced lesions lack the degree of anatomical precision desired, this study is nevertheless a compelling example of the impact of cerebellar damage on the cognitive-appraisal related component of emotion processing. In contrast, Clausi and colleagues (2015) assessed cerebellar patients and found that their risk-taking behaviour was not impaired, but did observe a reduction in patients' conscious experience of regret. Interestingly, autonomous physiological measures were unimpaired, suggesting a dissociation between cerebellar contributions to the arousal component of emotion and the cognitive appraisal-related component (Shuman et al., 2013). The cerebellum's contribution to cognitive aspects of emotion processing also extends to high-level social-emotional tasks that require complex

cognitive reasoning (see chapter 17: "Cerebellum and Emotion in Social Behavior"). For instance, several imaging studies have revealed involvement of the posterior cerebellar hemispheres in concert with several cerebral association areas, in social mirroring and mentalising tasks (Buckner et al., 2011; Van Overwalle et al., 2014). Moreover, neuropsychological reports of patients with cerebellar degenerative atrophy revealed behavioural profiles characterized by impairments in social perspective-taking, which were further accompanied by reduced functional connectivity between posterior cerebellar lobules and cortical regions involved in social-emotional reasoning (Clausi et al., 2019).<sup>3</sup>

Several subtheories have aimed to explain the cerebellar contribution to specific cognitive processes, such as aiding the detection of sequences (Molinari et al., 2008) or supporting the learning of associative relationships (Ernst et al., 2019; Timmann et al., 2010). As mentioned earlier, however, most of those proposals can be incorporated into the overarching idea that the cerebellum is crucial for the formation of internal models of the world for the prediction of future events (Ito, 2008; Miall & King, 2008). Applied to cognitive appraisal processes, this implies that the cerebellum supports the swift and accurate classification and recognition of emotional valence. Ferrari and colleagues (2018) provided support for this suggestion using a non-invasive brain stimulation approach (see Tomlinson et al., 2013 for an overview on cerebellar brain stimulation). More specifically, they found that transient virtual lesions of the cerebellum, via transcranial magnetic stimulation, led to reduced accuracy in explicit and implicit measures of emotion recognition. Their task required 36 participants to judge the emotional expressions and the gender of male and female faces. In comparison to an occipital control site, stimulation of the cerebellum significantly impaired appraisals of facial

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<sup>3</sup> For a review on the role of the cerebellum in perspective taking and embodied emotional-cognitive processes see chapter X: "Cerebellum, Embodied Emotions, and Psychological Traits"

expressions. Interestingly, cerebellar stimulation also affected implicit appraisal processes, since gender judgments for emotionally expressive faces, but not neutral faces, were also impaired. This finding suggests that if cerebellar support for emotional appraisal is disrupted, other emotion-related brain areas (such as the prefrontal cortex) must compensate, affecting accuracy for other cognitive operations. Complementary evidence for a cerebellar contribution to swift emotional appraisal processes comes from another brain stimulation study, which applied a weak, tonic direct current to the cerebellum (Ferrucci et al., 2012). Relative to a sham (i.e., no stimulation control) condition, cerebellar direct current stimulation led to a significant reduction in response time for the identification of facial expressions of emotions. Interestingly, this effect was only observed for negative but not positive facial expressions, which could be explained by the fact that negative stimuli generally evoke more robust physiological and behavioural responses than neutral or positive events (Fox et al., 2000). Moreover, from a perspective of survival optimisation, fear and anger are expected to be more directly related to fast behavioural actions than positive emotions, i.e., the former are highly time-critical responses (Mobbs et al., 2015).

Taken together, several lines of evidence suggest that the cerebellum is involved in the cognitive component of emotion, leading to a faster and more accurate appraisal of emotional stimuli and situations. Cognitive-emotional processes are predominantly underpinned by the posterior cerebellar hemispheres, in contrast to the arousal related aspects of emotion which are associated with the vermal regions (Adamaszek et al., 2017; Leggio & Olivito, 2018).

## Discussion

The preceding sections we have presented evidence to suggest that the cerebellum contributes to distinct components of emotion processing. These include physiological responses that contribute to the subjective or “feeling” component of emotion, emotional expressions that serve essential social-communicative functions, and the cognitive appraisal process that determines whether stimuli and context elicit emotions and, if so, what type. Moreover, the evidence is in line with the universal hypothesis of cerebellar functioning, which suggests that the cerebellum optimises functioning by providing accuracy, consistency, and appropriateness to cognitive and affective functions, as it does for movement-related operations (Adamaszek et al., 2017; Baumann et al., 2015; Koziol et al., 2014; Nixon, 2003; Schahmann, 2019).

While the idea of a cerebellar role in the regulation of emotion was originally spurred by patients with neurodegenerative disease (e.g., ataxia) and stroke (Schmahmann 2004), it is important to note that more recent neuroimaging studies have shown cerebellar abnormalities in several neurological and psychiatric conditions, including depression, bipolar disorder, anxiety disorder, schizophrenia and autism (Baldacara et al., 2008; Konarski et al. 2005; Moberget and Ivry, 2019)Stoodley & Schmahmann, 2010). The link with autism appears to be particularly strong. Wang and colleagues (2014) reviewed several lines of evidence showing that damage to the cerebellum in early human development is related to an increased risk of developing an autism spectrum disorder later in life. The resulting deficits, such as hypersensitivity to sensory stimuli, have been interpreted as due to a deficit in cerebellar internal models that predict external events, such as the sensory consequences of behaviour (Sinha et al., 2014). In the absence of temporally precise forward models,

neocortical learning and control processes are reliant on slower feedback control mechanisms (Parrell et al., 2017). Moreover, neuroimaging data suggest that even in the normal population, macro- and micro-structural variations in cerebellar areas are linked to variations in personality and mood. For instance, Laricchiuta and colleagues (2014) used MRI to investigate links between volumetric differences in the cerebellum and personality factors. They found that increased cerebellar volume was linked to higher novelty-seeking tendencies (i.e., increased risk-taking behaviour and sensitivity to rewards), whereas decreased cerebellar volume was associated with higher harm avoidance tendencies (i.e., excessive worrying and pessimism). Considering the universal theory of cerebellar function, these findings suggest that the cerebellum provides internal models of social-cognitive contexts and behaviours that become increasingly accurate and eventually allow behaviour responses to become faster, more precise, and independent of cortical control. The findings are also in line with the continuum hypothesis of mental disorders, namely, that personality traits can range from healthy interindividual variability to abnormal and harmful behavioural profiles (Sommer, 2010). Previous studies have shown that individual differences in one's disposition to experience negative emotions can be partially explained by differences in white-matter fibre connections in emotion-related brain networks. For example, trait anxiety in healthy populations has been found to correlate with white-matter microstructure in amygdala-ventromedial prefrontal pathways (Kim & Kim & Whalen, 2009). An important goal for future research is to investigate whether individual differences in structural connectivity of the cerebellum are related to variations in the disposition to experience negative emotions and the ability to regulate them.

Human neuroimaging has provided valuable insights into the functional anatomy and connectivity of the human cerebellum (Baumann & Mattingley, 2012; Guell et al., 2018; Habas

et al., 2009; Habas, 2010; Habas, 2021; Habas & Manto, 2018; Stoodley & Schmahmann, 2018). Nevertheless, neuroimaging techniques lack the spatial and temporal precision of invasive axonal tracing and single-cell recording techniques. Therefore, some uncertainty remains regarding the precise functional anatomical and structural connectivity of the human cerebellum. Uncovering the precise functional map and connection parameters of the cerebellum in healthy humans will enhance diagnostic classification and treatment response predictions in individual patients, which will allow clinicians to identify subgroups of patients with distinct pathophysiological causes of emotional dysregulation.

### Conclusion

The cerebellum makes an essential contribution to emotion processing, by facilitating accurate and context-sensitive emotional responses. Our chapter has reviewed various lines of evidence indicating cerebellar contributions to all sub-components of emotion processing, including physiological responses that contribute to the subjective or “feeling” component of emotion, emotional expressions that serve essential social-communicative functions, and the cognitive appraisal process that determines the emotional significance of events and therefore affects the generation and modulation of emotions. Future research aimed at unravelling the functional neural architecture of emotion processing is needed to refine theories posited to explain deficits in emotion regulation in neuropsychiatric disorders associated with cerebellar abnormalities (Konarski et al. 2005). Broader recognition of a cerebellar role in emotional processes will help to identify emotional deficits that at present may go undiagnosed in clinical groups, and will ultimately aid the development of targeted interventions.

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