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The Emotional Cerebellum

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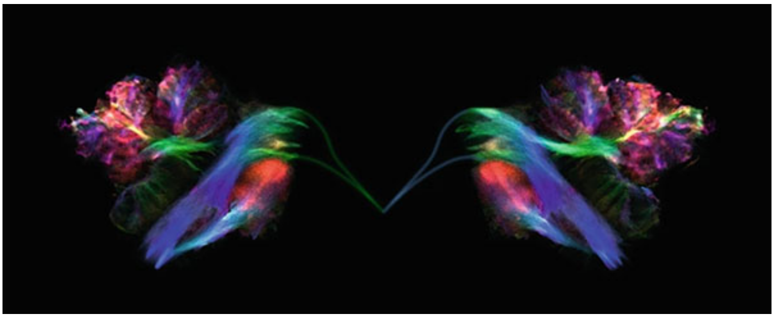

Hummingbirds. Colour-coded tract-density images generated from 0.8 mm diffusion-weighted MRI in a single healthy participant. Sagittal slices include depictions of fibres in the brainstem (coloured blue, running infer/superior), pons (red, medial/lateral), and cerebellum—with the superior cerebellar peduncle in green traversing from the cerebellum into the brainstem. 2021, Christopher J. Steele, Concordia University, Montreal, Quebec, Canada

Foreword

Homo sapiens

Cerebellum research is at a point where the close ties between the social-emotional cerebellum and the evolutionary rise of *Homo sapiens* can begin to be revealed. This idea is strongly supported by the detailed and verifiable paleontological analysis of the progression of socially, emotionally intense stone-tool making and the resultant capacities of the social-emotional cerebellum. These capacities drive uniquely human cumulative culture, the accumulated elaborations of culture we all share. The relatively new discipline of neuroanthropology (the study of the relationships between the brain and cumulative culture) proposes that the progressive evolution of stone-tool making was largely behind the evolution of *Homo sapiens*. This paleontological story can suggest that it is the social and emotional prediction capacity of the cerebellum that is to a very great extent behind the sapience we see in the astounding mental and technological elaborations of cumulative culture.

Linnaeus (1758) with limited knowledge of the brain in his time could only roughly refer to our species, with its great accumulation of culture, as *Homo sapiens*. However, the collective significance of the chapters of this book provides evidence that strongly supports the idea that the emotional, cognitive, and social functions of the *cerebellum* can be said to be the fundamental key behind our unique human ability to constantly move toward an optimized cumulative culture. With the tremendous advances in just how the cerebellum contributes to the rise of our cumulative culture consisting of everything from art, music, language, and mathematics to technology that mimics the mind (computers), perhaps it is time to embrace the massive contributions of the cerebellum as Linnaeus might have if he had known what cerebellum research and the authors of this book have provided—might he have understood that the cerebellum plays many key roles in our understanding of the meaning of the “sapience” of *Homo sapiens*?

To stress the important, undeniable relevance of neuroanthropology to the chapters in this book, an example of how learning stone-tool making critically involved social and emotional prediction and control by cerebellar internal models for approximately 2. 6 million years (1.7 million years for advanced stone tools) of adaptive selection is presented. Neuroanthropologists Stout and Hecht’s (2017) careful and detailed study of the extended repetitive practice necessary to stone-tool making is quoted at length so as to make its processes clear to a broad audience of both old and new to cerebellum research. Stout and Hecht refer to stone-tool making as "high fidelity" (imitative) social learning. As an example of this high fidelity social learning they describe how it takes place during the interaction between the learner and the teacher—that is, as we now know, how this interaction is modeled in the cerebellum:

> Knapping is a "reductive" technology involving the sequential detachment of flakes from a stone core using precise ballistic strikes with a handheld hammer (typically stone, bone, or antler) to initiate controlled and predictable fracture. This means that small errors in strike execution can have catastrophic, unreversible effects [*Thus (1) requiring intense-precise elaboration of theory of mind (ToM) which the learner must apply to the likely mental processes of the teacher, and (2) shaping emotional-motivational states in the learner's autobiographical knowledge base—i.e., knowledge of past and future action/interaction sequences related to the self*[1]]. Experiments by Bril and colleagues have shown that fracture prediction and control is a demanding perceptual-motor skill reliably expressed only in expert knappers. Building on this work, Stout and colleagues found that even 22 mo ($\bar{x} = 167$ h) of knapping training produced relatively little evidence of perceptual-motor improvement, in contrast to clear gains in conceptual understanding. (Stout and Hecht, 2017, Vandervelt L., 2019)

> The key bottleneck in the social reproduction of knapping is thus the *extended practice* [italics added] required to achieve perceptual-motor competence. This requires mastery of relationships, for example between the force and location of the strike and the morphology, positioning, and support of the core, that are not perceptually available to naïve observers and cannot be directly communicated as semantic knowledge. Attempts to implement semantic knowledge of knapping strategies before perceptual-motor skill development are ineffective at best, and such knowledge decays rapidly along knapping transmission chains when practice time is limited, even if explicit verbal teaching is allowed. *For observational learning, the challenge is to translate visual and auditory information of another's actions to appropriate motor commands for one's own body. This may be accomplished by linking the observed behavior with preexisting internal models* [Stout and Hecht are referring here to internal models in the cerebral cortex and not in the cerebellum] *of one's own body and actions through associative learning and stimulus generalization* [italics added]. Novel behaviors are copied by breaking them down into familiar action elements (e.g., lift, turn, twist), matching these, and reassembling. (pp. 7862-63). (Stout and Hecht, 2017, Vandervelt L., 2019)

We now know that what Stout and Hecht referred to as associative learning and stimulus generalization in the italicized portion immediately above are more correctly understood as the learning of internal models in the cerebellum. While Stout and Hecht did not mention the cerebellum in their research, the implications of this 2.6/1.7 million years of socially driven adaptive focus of thousands of generations of learners on the detailed bodily movement and facial expressions of the teacher for the evolution of the social cerebellum are obvious.

At the beginning of their above quote, Stout and Hecht (2017) pointed out that learning highly repetitive stone-tool knapping is a situation where "small

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[1] In keeping with the stone-tool evolution view of the evolution of autobiographical knowledge, it is important to point out that autobiographical knowledge consists of components which span (somewhat in the order of increasing optimization of forward control) the evolution of *Homo sapiens*, namely, spatial-visual, semantic episodic, and semantic conceptual. See Martinelli P, Sperduti M, & Piolino P. (2013). Neural substrates of the self-memory system: new insights from a meta-analysis. *Human Brain Mapping,* 34: 1515–1529. DOI: 10.1002/hbm.22008 for a discussion of these components of autobiographical knowledge.

errors in strike execution can have catastrophic, unreversible effects." For the learner, anticipation of such catastrophic effects would be quite emotionally stressful, and even for accomplished stone knappers this anticipation and emotional stress would be present, but controlled by elements of autobiographical knowledge (e.g., semantic knowledge of autobiographical knowledge manipulated in self-talk) containing the likelihood of predictive precision. Thus, cerebellar control of emotion during both this stressful social observation and solitary practice would have been selected in the evolving cerebellum.

Astonishing Parallels from Cerebellum Research

Although arrived at through a completely different disciplinary perspective, this idea and the italicized portions of the above quote fit astonishingly well with Van Overwalle, Manto, Leggio, and Delgado-Garcia's (2019) description of the social cerebellum's prediction of social-emotional states of others through the learning of theory of mind (ToM) and its relationship to the likewise cerebellar construction of an autobiographical self. ToM refers to one's mental simulative capacity to make inferences about the mental states of others. Van Overwalle, Manto, Leggio, and Delgado-Garcia argued that the cerebellum plays the following roles in the construction and manipulation of ToM and autobiographical knowledge:

> We hypothesize that the cerebellum acts as a "forward controller" of social, self-action and interaction sequences. We hypothesize that the cerebellum predicts how actions by the self and other people will be executed, what our most likely responses are to these actions, and what the typical sequence of these actions is. *This function of forward controller allows people to anticipate, predict and understand actions by the self or other persons and their consequences for the self, to automatize these inferences for intuitive and rapid execution, and to instantly detect disruptions in action sequences*. . .. The cerebellum would be a "forward controller" that not only constructs and predicts motor sequences, but also takes part in the construction of internal models that support social and self-cognition. In this respect, the cerebellum crucially adds to the fluent understanding of planned and observed social interactions and contributes to sequencing mechanisms that organize autobiographical knowledge. Because the fundamental organization of the cerebellar circuitry is identical in many species adopting social behaviors, our hypothesis can also be valid throughout the animal kingdom. (p. 35) (Van Overwalle F, Manto M, Leggio M, Delgado-García, 2019, Vandervelt L., 2019)

Elsewhere in their 2017 earlier quoted article Stout and Hecht argued that the learning of stone-tool making required a good share of both observational learning of sequences of action (as described directly above) and *solitary* practice to refine the details necessary to those sequences; they suggested deliberate practice. In deliberate practice as described by Ericsson, Roring, and Nandagopal (2007), the learner focuses attention on self-perceived weak aspects of their performance that are related to the attainment of the teacher's level of performance. It is my view that autobiographical knowledge is what was adaptively selected in the evolution of this powerful and necessary solitary practice, because it resulted in learners that were both motivated and able to institute self-driven practice toward the level of precision and goal attainment they had observed in the teacher. As a footnote here, it is important to note that Van Overwalle et al.'s above final sentence concerning organization of cerebellar circuitry throughout the animal kingdom would of course apply to any species of early Homo that originated stone-tool making 2.6/1.7 million years ago (i.e., any pre-Homo *sapiens* species).

These overall connections place the evolution of stone-tool making as a verifiable framework through which to further understand why the cerebellum would be importantly involved in emotional aspects of theory of mind and autobiographical knowledge and therein to possibilities of disorders as described by Schmahmann's "cerebellar cognitive affective disorder" (CCAS). The importance of these points, while providing important evolutionary background for cerebellum researchers, is that it can alert whole new audiences of readers to the chapters of this book and to their significance in understanding the roles of the cerebellum in the evolution of cumulative culture. It does this specifically because it reveals where and how advances in ToM and linked autobiographical knowledge that are essential to the motivation for solitary practice (and resultant skill optimization) took place in the cerebellum among *Homo sapiens*. Since these cerebellar capacities can reasonably be seen as the marks of our species' evolution of progressive cumulative culture, this suggests that in actuality we are to a great extent *Homo sapiens* due to the evolution of the social/emotional contributions of the cerebellum. This newer understanding of *Homo sapiens* can focus study on new aspects of the prehistory, history, and future development of our species. The chapters of this book represent important steps in that direction and should be of strong interest to a broad audience of readers including those in anthropology, cognitive neuroscience, neuroanthropology, psychology, and a variety of studies of deliberate practice in the field of education.

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Part I

Basic Principles of Cerebellar Function in Emotion

1 Introduction into the Role of the Cerebellum in Emotion

Michael Adamaszek, Mario Manto, and Dennis J. L. G. Schutter

Abstract

The cerebellum is well known for its contribution to motor performance, but less for its involvement to cognitive and affective processing. The growing interest of clinical and neuroscientific research has resulted in a fascinating focus on the cerebellar mechanisms of emotion. Advances in functional neuroimaging and noninvasive stimulation protocols have successively delineated circumscribed cerebellar areas with its functional and topographic connections to the conventionally predominating cerebral cortex in basic as well as high order emotion processing. This encompasses all information processing stages which include perception and attention, and the evaluation and integration of emotion cues to the trajectories in motor, cognitive, and affective behavior. Not surprisingly, research has identified the cerebellum being part of the brain's network associated with art, morality, and social cognition. This book will provide an overview of the details of these intriguing issues, supporting a contemporary understanding of the fundamental as well as specific features of cerebellar functions within emotion processes.

Keywords

Behavior · Cerebellum · Emotion · Neuroscience · Psychology

The cerebellum with its role in mental functions gains considerable attention in the rapidly expanding field of fundamental and clinical neuroscience. The previously predominant understanding of the cerebellum was in the context of motor-related behavior and considered to be the sole cerebellar function in clinical neurology. However, this traditional view is now increasingly challenged and the cerebellum is now receiving increasing attention by the scientific community as a brain region that contributes to a broad spectrum of non-motor areas as well. The idea that the cerebellum plays a role beyond being a hub within the complex neural networks of the primary and supplementary motor cortex is to a significant extent due to modern experimentation, such as functional magnetic resonance imaging, which has revealed cerebellar involvement in neural processes of related non-motor behaviors. These discoveries have led to a critical review and reappraisal of the classical view of the cerebellum

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as entirely a motor-dedicated region in the last three decades. The view that the cerebellum is a brain structure primarily devoted to motor functions is no longer attainable.

The idea that the cerebellum is also involved in the perception and processing of emotions is not new and can already be traced back to early observations in the 1940s, potentially representing a first step toward a systematic neuroscientific evaluation on this idea. For example, Moruzzi (1941, 1947) and also Zanchetti and Zoccolini (1954) reported autonomic hypothalamic outburst and rage-like behavior in response to electric stimulation of the cerebellum. These findings concur with a subsequent outlining of Anand et al. (1959) that the cerebellum has connections to the limbic system, providing a neuroanatomical basis for a role in the emotion-dedicated subcortical circuits. Just a few years later, Prescott (1970) hypothesized that the cerebellum is involved in virtually all aspects of emotion, acting as a "master integrator of regulatory systems for sensory-emotional and motor processes." This concept reflects the growing systematic investigation within neuroscience, provided by the following research line of Heath and his findings on cerebellar implementation in affective behavior (Heath et al. 1978; Heath et al. 1980). Furthermore, Leiner et al. (1986 and 1989) in the 1980s outlined the observations that in parallel with the cerebral cortex the cerebellar hemispheres and dentate nuclei underwent huge volumetric expansions in the course of human evolution. These observations provide a possible phylogenetic account for the involvement of the cerebellum in cognition and emotion. Leiner et al. hypothesized that these cerebellar regions project to prefrontal and other association cortices in humans and higher primates, forming closed cerebello-cortical loops (Fiez 1996). It was suggested that cerebellar damage could compromise the integrity of the cerebello-cortical system and as a net result leads to cognitive impairments (dysmetria of thought). This possibility was further elaborated by the pioneering work of Schmahmann that started back in the 1990s and has continued to the present day (Schmahmann and Sherman 1997, 1998; Schmahmann 2010; Schmahmann et al. 2019). In line with the fast development of experimental human brain research from the 1990s onward, empirical studies confirmed that the cerebellum contributes to high-level cognitive and affective domains. Indeed, the large body of available scientific data indicates that the cerebellum is part of the distributed cortico-limbic networks involved in perception, attention, language, appraisal, feelings, and cognitive control and regulation processes as part of the brain's executive functions (Habas et al. 2009; Buckner 2013; Schmahmann et al. 2019). In terms of the evolutionary trajectory of the human brain, there is some evidence that both the parietal cortex and the cerebellum have undergone the comparatively largest growth rate in terms of developmental history (Neubauer et al. 2018), which is unlikely a coincidence. At the same time, the strong forward and feedforward connections between the prefrontal cortex and the cerebellum were highlighted in various works (e.g., Middleton and Strick 2001). Indeed, research in primates has successively outlined that the posterior and particularly the lateral parts of the cerebellum have expanded disproportionately in the human brain, and are interconnected with the cerebral cortex covering a wide range of attention and control-related functions of the fronto-parietal networks (Strick et al. 2009; Marek et al. 2018). Involvement of the cerebellum in development of visuospatial processing, working memory, executive functions, theory of mind, and the conscious experience of emotions and feelings is suggested to stem from an increase in social interactions and communication when humans transitioned from living in solitary to living with fellow members and form groups (Neubauer et al. 2018; Marek et al. 2018).

The cerebellum or little brain is a neural structure located in the posterior fossa of the skull beneath the tentorium and the occipital lobe of the cerebral hemisphere (O'Hearn and Molliver 2001). The adult human cerebellum accounts for approximately ten percent of total brain volumes. Despite its modest size, the cerebellum contains more than half of the total neurons present in the human brain (Azevedo et al. 2009).

Phylogenetically, the posterolateral parts of the cerebellum have, in concert with the cerebral cortex, undergone a rigorous volumetric expansion (Balsters et al. 2010; Weaver 2005). Interestingly, a recent successful attempt to unfold the complex and intricated cerebellar cortex revealed that its surface is almost 80 percent of the total surface of the cerebral cortex (Sereno et al. 2020). In addition to the three-layered cortex, the cerebellum consists of deep cerebellar nuclei (DCN) and white matter (O'Hearn and Molliver 2001). The DCN consists of four paired deep gray matter nuclei called (1) the fastigial nuclei, (2) the globose nuclei, (3) the emboliform nuclei, and (4) the dentate nucleus. Together they form the sole output regions of the cerebellum. The relatively homogenous cellular composition of the cerebellar cortex comprises an outer molecular layer made up of axons and dendrites of cerebellar neurons and interneurons consisting of basket and stellate cells, a Purkinje cell layer, and a granular layer made up of granule cells and Golgi interneurons. In terms of its evolution, the cerebellum can be divided into three more or less distinct regions: the archicerebellum (flocculonodular lobe), paleocerebellum (anterior part of the cerebellum and vermis), and neocerebellum (posterolateral hemispheres) (O'Hearn and Molliver 2001). The archicerebellum, the phylogenetically oldest part of the cerebellum, is connected to the vestibular system and reticular formation in the brainstem. The paleocerebellum has connections to the spinal cord, brainstem, as well as subcortical structures (Schutter 2013). The neocerebellum as the phylogenetically youngest part of the cerebellum is evolved in concert with the cerebral cortical association areas to form closed cerebello-thalamo-cortical loops (O'Hearn and Molliver 2001). While there exist several taxonomies, the cerebellum is most commonly divided into a series of lobes and lobules. The anterior lobe consists of lobules I–V and is anatomically separated from the posterior lobe by the primairy fissure, whereas the posterior lobe consists of lobules VI, Crus I and II, VIIB, VIII–IX, and the flocculonodular lobe has been labeled lobule X, respectively (O'Hearn and Molliver 2001).

The trafficking of incoming and outgoing signals occurs along three white matter bundles known as the cerebellar peduncles. The inferior cerebellar peduncle (restiform body) is a cordlike bundle of afferent and efferent white matter fibers that connects the medulla oblongata with the cerebellum. The middle cerebellar peduncle (brachium pontis) connects the cerebellum to the pons and is composed entirely of afferent (input) fibers. Finally, the superior cerebellar peduncle (brachium conjunctivum) consists of efferent fibers and constitutes the output channel of extracerebellar areas. Figure 1.1 shows the main anatomical components of the cerebellum.

The notion of cerebellar contributions to human emotions was decisively established by the seminal neuropsychological study by Schmahmann and Sherman (1998). The authors assessed in detail the clinical findings of cognitive impairments as well as changes in affective behavior following cerebellar lesions. The so-called cerebellar cognitive-affective syndrome (CCAS) or Schmahmann's syndrome has been validated by a multitude of clinical and imaging studies. The corresponding affective components of Schmahmann's syndrome include personality changes, behavioral disinhibition, inappropriate behavior, altered mood regulation, anger, blunting of affect, pathological crying and laughter, obsessive-compulsive tendencies, and psychotic thinking (Schmahmann 2004). The emotional disturbances were mainly observed in relation to damage to the vermis, which predominantly projects to autonomic, reticular, and limbic brain regions. The number of neuroimaging studies on the individual topographic and temporal connections of certain domains of emotion processing has led to a rethinking of the neural mechanisms underlying the recognition, experience, and regulation of emotions (Schutter, 2019). In the meantime, the significance of the prefrontal cortex (PFC), notably the dorsolateral prefrontal cortex (DLPFC), orbitofrontal (OFC) and ventromedial (vMPFC), and the anterior cingulate cortex (ACC) in the attention, motivation, and emotion-related processes, has been established. Furthermore temporally and spatially bound activities of subcortical areas such as the amygdala and sections of the basal ganglia have

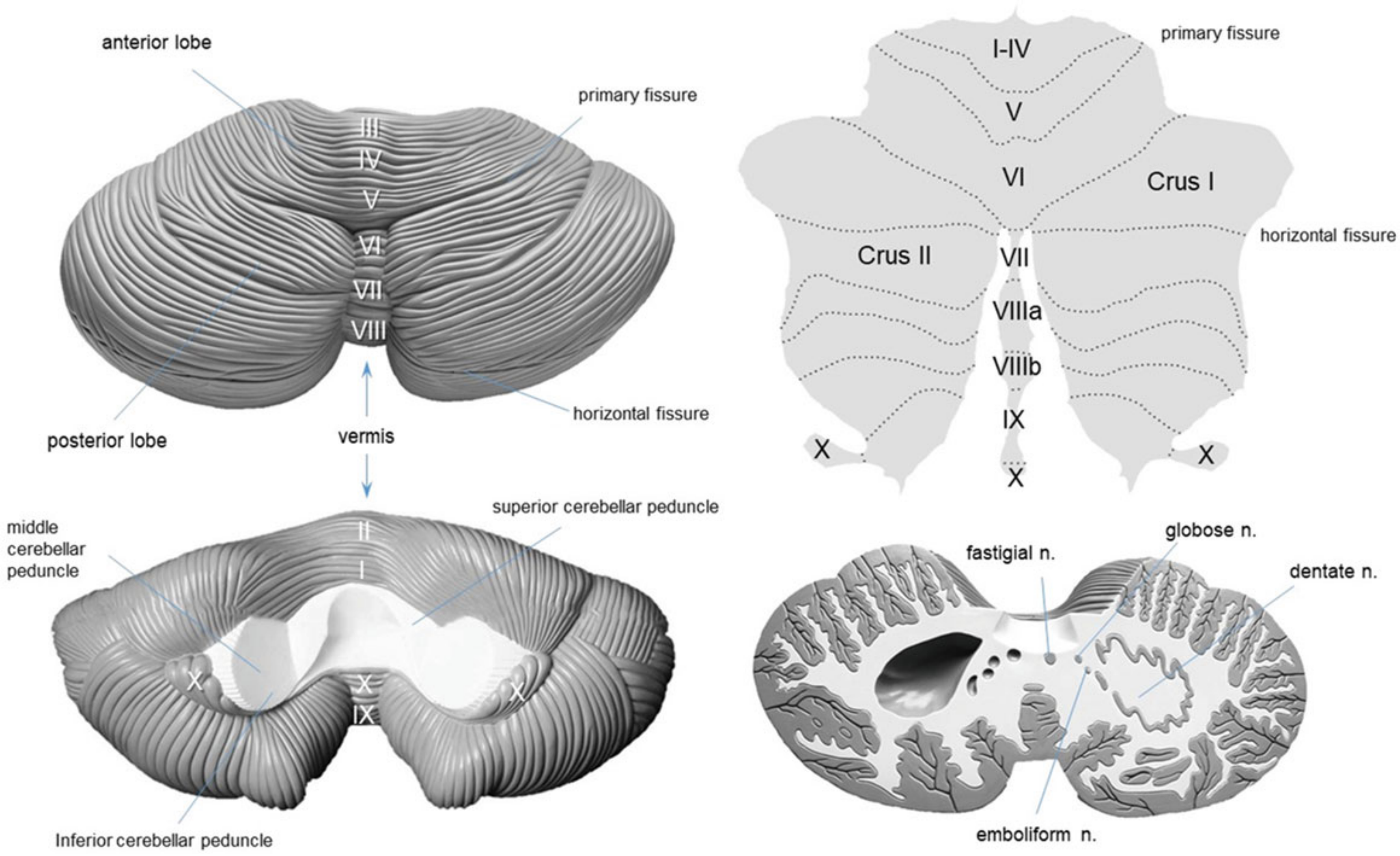

Fig. 1.1 Gross neuroanatomy cerebellum

been highlighted (LeDoux 2000; Pessoa 2013). Along the growing awareness to functionally integrate the various subcortical and cortical networks to better understand the neurological basis of emotion, the cerebellum is increasingly recognized as playing a significant role in this functional integration process (Stoodley and Schmahmann 2009; Buckner 2013; Adamaszek et al. 2017). It can now be readily assumed that distinct areas of the cerebellum are part of distinct cerebello-cortico-limbic circuits, integrated in larger, broadly extending networks with a focus within cerebral fronto-parietal, fronto-temporal, and parieto-temporal axis systems of the brain. These axes arguably represent higher-order associative connections as the neural basis of the individual functional performances of specific cognitive and affective domains (Schmahmann 2010; Adamaszek et al. 2017; Argyropoulos et al. 2020; Schmahmann et al. 2019).

Based on the work of Schmahmann as well as the systematic investigations of other groups worldwide, the existence of discrete functional areas of the cerebellum has paved the way for new insights into cognition- and emotion-based higher order mental phenomena that include empathy, theory of mind, moral judgment, and action. Indeed, several individual posterior cerebellar sections, including lobule VI, Crus I and II of lobule VII, and also parts of lobule VIII, have been shown to be embedded in a complex system consisting of a wide array of neural circuits that operate as functional modules in a decentralized, highly parallel fashion selectively engaged by environmental demands to produce adaptive behavior (Ito 2008; Schmahmann et al. 2019). The importance of the cerebellum in emotion and social cognition is further illustrated by the growing number of empirical studies (Van Overwalle et al. 2020). For example, a large number of available scientific studies have established the significance of the cerebellum as part of distinct neural networks in the recognition and processing of emotional facial expressions (Kilts et al. 2003; Fusar-Poli et al. 2009; Schutter et al. 2009; D'Agata et al. 2011; Ferrucci et al. 2012; Adamaszek et al. 2014, 2015). Yet, other studies have examined the contributions of the lateral hemispheric regions of the cerebellum for attending to emotionally laden salient cues (Adamaszek et al. 2013; Turner et al. 2007; Styliadis et al. 2015). Results showed that predominantly posterior parts of the cerebellum, including vermal area of lobule VII with its Crus I and II, contribute to the discrimination of salient cues as well as facial and acoustic expressions of emotions across different valence and arousal levels. Even though the contributions of the vermis and fastigial area of the deep cerebellar nuclei were not considered, the relationship between the neocerebellum and the predominantly prefrontal and parietal components of emotion recognition in particular to its inclusion of affective ingredients in object perception and evaluation further underlines the functional significance of the cerebellum in emotions.

A turning point in the transition from the motor-centered view toward a modern understanding of the cerebellum as a distinct part of the neural circuits dedicated to higher-order processes may have been the work by Parsons and Bower during the end of the nineties of the last century and the first decade of this century. Their observations and reflections on cerebellar activities and sensory process pathways introduced a new way of thinking with a greater focus on sensory-receptive and integrative functions of the cerebellum (Parsons et al. 2009). This novel approach is in agreement with the idea that the posterior cerebellar hemispheres and their functional connections to the parietal and prefrontal regions play an active role in the regulation of task-related activity of the specialized cerebral networks. Moreover, the integration and control of cognitive and affective contextual factors of a perceived sensory event are of further importance for selecting the optimal behavioral response. To this end, the responsible cerebral fronto-parietal networks arguably include reciprocal pathways to specific locations in the vermis and posterolateral hemispheres of the cerebellum (Leiner et al. 1986; Ivry and Fiez 2000; Demirtas-Tatlidede and Schmahmann, 2013; Argyropoulos et al. 2020). In support of the latter notion, the posterior parts, especially lobule VII with Crus I and II, in cognitive and affective tasks, but also vermis and its connections to the limbic networks, are assumed to be involved in the processing of visceral, autonomic, and other emotion-relevant information (Habas et al. 2009 and Adamaszek et al. 2017; Stoodley and Schmahmann 2009; Koziol et al. 2014). Considering the putative role of the cerebellum within the presumed cerebello-cortical integration of functions, the cerebellum deems to support the brain's operative and predictive functions. In addition, the cerebellum is considered to be part of an internal model in which specific cerebellar units guide the precise representation of sequential and temporal information of exteroceptive and interoceptive signals in response to task-related cognitive and affective processes (Ito 2008). According to Ito (2008), the cerebellum with its evolutionary developed access to specific neural network provides a synchronized tracking and controlling of the interrelated activities between the perception of an object and its subsequent processing stages. This particular neural tracking is supposed to be in dependency of different manipulations of mental representations within specialized cerebellar areas in favor to gain an optimal behavioral response based on the integration of sensory, affective, and cognitive signals. This might even represent a fascinating and animating hypothesis that would fit the idea of specific cerebellar contributions to executive networks in face of increasing function complexity (D'Angelo and Casali 2013; Adamaszek et al. 2017), regulating the speed, smoothness, and finally the appropriateness and accuracy of the processes in the cerebral cortex, providing for a skillful execution including its related affective constituents during the early and late processing stages (Leiner et al. 1986; Schmahmann 2010). Accordingly, the assumption of a central cerebellar executive, that is the active process of adapting ongoing behavior to subsequent and forthcoming sequelae, points to a generic property of a predictive interface in task-dependent neural networks to anticipatory adjustments at the level of the cerebral cortex to maximize current and future task performance (Ivry and Fiez 2000; Ito 2008). Moreover, this proposal is strengthened by empirical observations showing that cerebellum topographically maps to the central executive control networks (ECN), the default network (DMN) (Habas et al. 2009; Krienen et al. 2009; Brady et al. 2019), and attention networks (Allen et al. 1997; Akshoomoff and Courchesne 1994; Breska and Ivry 2020) (for an overview, see Table 1.1).

In keeping with the growing body of knowledge about the role of the cerebellum in high order mental functions of the brain, the "emotional" cerebellum might operate at several specific and non-specific levels along the responsible large-scaled networks along the lateral and medial prefrontal as well as parietal areas. Besides the structural and functional neuroanatomic descriptions with a focus on the vermis and paravermal areas, lobules VI–VIII including Crus I and II, and the deep cerebellar nuclei, the mechanisms of action, including its sequential and time-dependent operation modes, are of particular interest in decoding the cerebellar activation patterns associated with the generation, experience, and regulation of emotions. This volume offers novel and unique insights into the hitherto available positions of the contributions and responsibilities of the cerebellum in affective processing by covering the basic and advanced facts and notes in contemporary neuroscience. In this volume, we would like to take the reader on a journey that goes beyond the conventional cortico-limbic oriented theories of emotion. The structural and functional neuroanatomic foundation of the cerebellum in emotion is first discussed by Marine Thomasson and Julie Péron in Chap. 2. In Chap. 3, Oliver Baumann and Jason Mattingley provide an account of the cerebellum in emotion processing by separately evaluating its impact for components of emotion processing. These components include physiological responses, emotional expressions, and the cognitive appraisal processes that influence the generation, experience, and regulation of emotions. Federico D'Agata and Laura Orsi discuss the cerebellar correlates of emotion recognition in Chap. 4. Emotional learning and memory is the main topic of Chap. 5 covered by Melanie Mark, Johanna Pakusch, Thomas Ernst, and Dagmar

Table 1.1 Brain regions and associated (not exhaustive) main functional correlates discussed within the context of the cerebellum and emotion

	Structure	Associated functional correlate(s)
1	Amygdala	Relevance detector; emotional learning; emotion perception
2	Anterior cingulate cortex	Outcome anticipation; performance monitoring; vigilance
3	Striatum	Habit; learning; reward; action selection
4	Pallidum	Regulation of voluntary movement
5	Subthalamic nucleus	Suppression of unwanted movements
6	Substantia nigra	Dopamine production site; initiating movements; learning
7	Hippocampus	Learning; memory
8	Hypothalamus	Regulation of metabolic and endocrine processes; circadian rhythms
9	Insula	Disgust; taste; interoception; bodily homeostasis
10	Nucleus accumbens (ventral striatum)	Reward reinforcement; liking
11	Parietal cortex	Sensory integration; visuospatial attention
12	Pons	Regulation and control of vital bodily functions
13	Prefrontal cortex	Executive and regulatory functions
14	Reticular formation	Arousal
15	Septum pellucidum	Pleasure; reward; reinforcement learning; prosocial behavior
16	Temporal cortex	Language; object recognition
17	Thalamus	Relay station
18	Ventral tegmental area	Reward; sex; motivational salience; positive emotions; associative learning

Timmann who provide a comprehensive overview of the basic cerebellar mechanisms. The neurotopographical and neurophysiological aspects of the cerebellum will be covered in chapters 6–8. Christophe Habas will provide an overview of the complex neural topography of individual fiber bundles and their connections to the cerebral cortical networks within the context of emotion recognition, emotion processing, and behavior. Michael Adamaszek and Ken Kirkby focus on electrophysiological signatures of emotion recognition and processing to reveal their temporal dynamics in which the cerebellum plays an important role. Corresponding to the more spatial aspects as outlined by Christophe Habas, and the more temporal aspects of cerebellar involvement in the specific network activities in emotion processing as explained by Michael Adamaszek and Ken Kirkby, Jana Klaus, and Dennis Schutter elaborate on the now respectable knowledge of noninvasive brain stimulation approaches to the cerebellum in the modulation of emotion functions and the possible future therapeutic aspects of the treatment of emotion processing disorders. The third section of the book is devoted to the involvement of cerebello-cortical networks in higher-level domains of emotion processing. In Chap. 9, Jordan Pierce and Julie Péron discuss the role of the cerebellum in habit formation by way of monitoring and modulating precisely timed sequences of events using prediction and reward-based error feedback signals. In Chap. 10, Chiara Ferrari, Andrea Ciricugno, and Zaira Cattaneo provide an account of the cerebellum contribution to the processes underlying the complex details of body language perception and emotion. Chapter 11 authored by James Houston, Jahangir Maleki, Frank Loth, Petra Klinge, and Philip Allen in Chap. 11 addresses the growing insights of the cerebellum in various aspects of pain processing. In Chap. 12, Hyemin Han follows up by discussing what cerebellar aspects are known for the neural mechanisms of morality, and what the possible implications may be for ongoing and outstanding research. Specific functions of the cerebellum with regard to the brain's sensory processing pathways that, in addition to cognitive ones, have a high emotional component and separately characterize social development, which are highlighted in chapters 13 and 14. Stefan Evers and Bernadette Tölgyesi in Chap. 13 summarize the cerebellar features in neural networks of music perception, whereas Chap. 14 of Michael Adamaszek, Zaira Cattaneo, Andrea Ciricugno, and Anjan Chatterjee captures the hitherto little-known cerebellar functional components in the perception and processing of visual art and creativity. Silvia Clausi, Michaela Lupo, Giusy Olivito, and Maria Leggio summarize the complex body of empirical work on the cerebellum and social behavior, and offer explanations for cerebellar-based impairments in the social-affective domain related to neurological and psychopathological conditions. In Chap. 16, Daniela Laricchiuta, Eleonora Picerni, Debora Cutuli, and Laura Petrosini review their comprehensive work on cerebellar aspects of higher-order emotion processes and address how the embodiment approach may represent a unifying perspective for examining the cerebellar role in emotional behavior and psychological traits.

The fourth and final section of this volume deals in two separate chapters with aspects of the cerebellum that are particularly relevant for the clinical fields of neurology, psychiatry, and clinical psychology, and which therapeutic options currently might be feasible. Dennis Schutter presents in detail the clinical and imaging knowledge to date on the characteristics and peculiarities of emotion disorders, which are of significant importance especially with regard to clinical assessment and possible therapeutic applications. Kim van Dum, Mario Manto, and Raf Meesen conclude in their chapter on these clinical aspects of disorders of emotion recognition and emotion processing with a focus on the rehabilitative application possibilities, which have not been attempted in this form so far. In many respects, this chapter covers the often lamented discrepancy between the functional disorders described in clinical and neuroscientific work in the case of circumscribed or diffuse damage within the cerebellum and the necessary treatment possibilities of function restoration or compensation.

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Principles of Brain and Emotion: Beyond the Cortico-Centric Bias

2

Marine Thomasson and Julie Péron

Abstract

Affective neurosciences have largely contributed to the elaboration of theoretical and neuroanatomical models through research conducted in non-primate animals and human beings. However, for methodological and historical reasons, knowledge has developed by focusing mainly on the cerebral cortex, resulting in a lack of investigations of the functional aspects of subcortical structures such as the cerebellum and the basal ganglia. The close anatomical connections revealed between these two structures, as well as their reciprocal connections with the cerebral cortex, lead to a vertically organized model of the brain. Both the cerebellum and the basal ganglia are involved in the different components required during an emotional episode. Their respective specificity in the analysis of temporal patterns contributes to the optimal processing of emotional signals such as those that can be conveyed by the voice (emotional prosody). Internal temporally structured event representation, built from the salient modulation extractions performed by the cerebellum, is used by the basal ganglia to recruit and synchronize the activity of the cortical and subcortical structures required for the relevant processes.

Keywords

Basal ganglia · Cerebellum · Emotional prosody · Cortico-centric · Synchronization

2.1 Introduction

During the last century, affective neuroscience highlighted the complexity of affective processing from a conceptual and neuroanatomical point of view. Current studies have emphasized the involvement of large-scale brain networks in emotional processes, including the limbic system consisting of the thalamus, hypothalamus, hippocampus, amygdala, septum, and cingulate cortex, parts of the basal ganglia (e.g., striatum, internal and external segments of the pallidum), substantia nigra (pars reticulata and compacta), and subthalamic nucleus (Percheron et al. 2012), and finally the cerebellum (Bostan and Strick 2010; Anand et al. 1959). The role of the cerebellum and basal ganglia during emotional processes has been neglected until recently in favor of their motor contribution. The field of human affective neuroscience was indeed largely affected by historical and methodological barriers, discussed later in this chapter, which restricted the exploration of subcortical structures other than the amygdala, a phenomenon called

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the cortico-centric bias. However, in recent years, these obstacles have been overcome, mainly as a result of clinical neuropsychological observations in humans that have allowed researchers to develop theoretical propositions regarding the functional specialization and integration of brain networks beyond the cerebrum, including the basal ganglia and cerebellum, in the synchronization of emotion components. Indeed, componential approaches suggest that emotional processes are elicited and dynamically patterned by involving synchronized changes in distinct functional subsystems including those involved in motivation and motor expression.

In this chapter, we first present the appraisal theory of emotion and one particular model, the component process model (CPM), which is arguably well suited to model and study neural network-inspired approaches. CPM has shown to be particularly heuristic in the development of theoretical models of the functional role of subcortical structures during an emotional episode. In the second section, we show why the basal ganglia and the cerebellum have been neglected in affective neuroscience until recently. Finally, in the third section, we propose an original model, using the example of vocal emotion decoding (i.e., emotional prosody), in light of the different roles fulfilled by what has been called the “vertically organized brain” (Koziol and Budding 2009), which includes the cerebrum, the basal ganglia, and the cerebellum.

2.2 The Neuropsychology of Emotions: Insights from the Component Process Model Framework

Emotions play a central and special role within the cognitive system because most of the psychological mechanisms are either necessary for emotions, influenced by emotions, or involved in the modulation of emotions (Davidson et al. 2004). The models of emotions recently proposed are derived from theories of cognitive evaluation (appraisal) of emotion that suggest that cognitive processing was involved in the origin of emotions (Grandjean et al. 2008). From that perspective, many studies conducted in psychology have contributed to the conceptualization of emotion as a multicomponent phenomenon (Sander and Scherer 2014).

2.2.1 Emotion as a Synchronous Modification of Several Components

According to the CPM (Scherer 1984), emotions can be defined as episodes of synchronized changes occurring in an organism’s components that include physiological arousal, cognitive appraisal of the situation, subjective feelings, motor expression, and action tendencies (Grandjean and Scherer 2008). These dynamic processes are produced in response to environmental events, either internal (e.g., thoughts, sensations, or memories) or external (e.g., other people’s behavior or changes in situation), which are of significance to that organism (Scherer 2001; Sander and Scherer 2014). For example (see Fig. 2.1), after an individual hears a gunshot, changes will occur at the *physiological level* (e.g., blood pressure and heart rate increase, stress hormones such as cortisol and adrenaline are released); a *cognitive evaluation* of the event will occur (perceptual processing such as the distance from the gunshot, an understanding of the causes and consequences of the event, a link to the well-being and goals of the individual); and an expression of fear can appear on the individual’s face, with brow raising and jaw dropping at the *motor level*. In parallel, in this situation, particular *action tendencies* will be prioritized (e.g., avoidant behavior or search for outside help). In addition, a *subjective feeling* will emerge (“I’m afraid”) on the basis of the coupling between these components or of dimensions such as valence (i.e., pleasant vs. unpleasant) and arousal (intensity). Thus, when the components of emotion unfold in relative synchrony (or synchronization), a subjective feeling can emerge within an emotional episode and be perceived by the person at the conscious level (i.e., experience of a feeling at time t) (Glauser 2014).

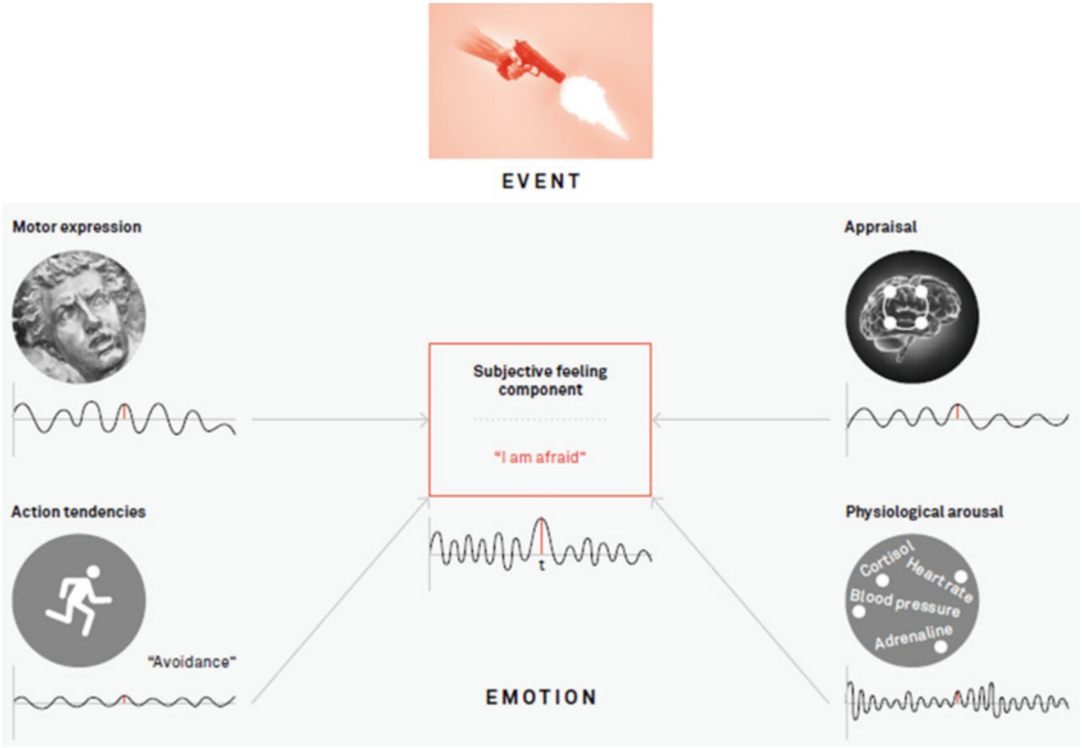

Fig. 2.1 Illustration of emotional component synchronization during the emergence of a subjective feeling following a specific event according to the component process model (Scherer 2001). The synchronization of the components of motor expression, arousal, appraisal, and action tendencies, at time t, allows the production of a conscious subjective feeling

This model therefore suggests processes of synchronization and integration between the different components, as well as parallel and sequential processing of information according to different evaluation criteria on different levels (for further details concerning the CPM, see Sander et al. 2005). Figure 2.1 provides a synthetic view of the theoretical psychological proposition of the CPM. This model invited affective neuroscience to identify the neuronal substrates involved in these different stages and components of emotion processing and to explore possible dissociations in clinical populations. It offered a heuristic model in the sense that the notion of synchronization proved to be particularly relevant in understanding the role of the basal ganglia (Péron et al. 2013) and the cerebellum (Pierce and Péron 2020).

2.2.2 Neural Basis of Emotion

Although the well-known circuit-level theory of emotion, proposed by Papez (1937) and completed by MacLean (1955), implicated some subcortical structures, it emphasized the cortical structures in the processing of emotions. The anterior nuclei of the thalamus, hypothalamus, septum, hippocampus, and amygdala were named on the subcortical side, and the cingulate cortex and prefrontal cortex were named on the cortical side. The role of cortical regions has been widely studied. For example, the ventromedial prefrontal cortex is involved in integration of diverse cognitive and emotional processes, as it has close connections with the anterior insular cortex and the amygdala (Gainotti 2020; Dixon et al. 2017). The anterior insula is reported to be involved in pain processing and empathy, as it is suggested to be an important region for integrating external and internal emotional information to form a “global emotional moment” (e.g., Craig 2009). In addition, the cingulate cortex was highlighted as a leading actor in emotional regulation in monitoring conflict between the functional state of the organism and any new information that has potential affective or motivational consequences (e.g., Bush et al. 2000). Nevertheless, the centrality of these structures in affective processes has been strongly criticized in view of the mainly cognitive and not exclusively emotional role that they could play (LeDoux 1998; Roxo et al. 2011). For example, the rostral anterior cingulate and anterior insula participate extensively in cognitive processes that are likely unrelated to emotion (Wager et al. 2008). Concerning the subcortical structures, the studies describing their role in affective processing are less numerous in the literature, with the exception of those concerning the amygdala. Indeed, the amygdala was considered one of the most important brain regions for emotion-related processes, with a key role in the processing of social signals of emotion (particularly those involving fear) (LeDoux 2003), in emotional conditioning, and in the consolidation of emotional memories (Phelps and LeDoux 2005). Moreover, the amygdala is a “relevance detector,” being involved in the appraisal and labeling of significant stimuli in the context of individual such as needs, goals, desires, and values that contribute to the elicitation of an emotion (for a review, see Sander et al. 2003).

Overall, most models advocate an overrepresentation of the cortex in emotional processes, with the exception of some subcortical structures such as the amygdala or the anterior nucleus of the thalamus. Indeed, as will be discussed in the next section, for both historical and methodological reasons, subcortical regions, currently recognized as being involved in human emotions, have been marginalized for a very long time.

2.3 The Cortico-Centric Bias in the Field of Neuropsychology of Emotions

The cortico-centric bias describes the tendency to see emotion as a production of the neocortex (Berridge 2009). This view was mainly adopted by theorists who studied emotions in human beings and primates, whereas scientists who studied emotional and motivational behavior in non-primate animals more strongly emphasized the role of subcortical structures in emotional processing (Berridge 2009). Thus, the differences generated by these two fields of research, both conceptually and methodologically, could explain the difference in emphasis between cortical and subcortical regions for emotion processes.

2.3.1 On the Origins of the Cortico-Centric Bias of Emotions

According to Berridge (2009), a *first* argument in favor of this cortico-centric view is that the emotional tasks used in human affective neurosciences most of the time require high-level cognitive judgment (e.g., recognize and label the expressed emotion), whereas most of the tasks in animal studies use more “primary” stimuli such as conditioned stimuli. This argument implies that correlational studies conducted in humans are more driven by the involvement of cognitive processes, as humans are more likely to use cortical regions, whereas studies in animals are more likely to be driven by subcortical regions. *Second*, technical constraints of imaging studies are also a reason for this cortico-centric vision. For example, magnetic resonance imaging (MRI) or positron emission tomography techniques are designed to detect changes in blood flow/metabolism in specific regions that are spatially organized. We could thus think that cortical regions, being more spatially segregated, are more likely to be detected as activated during an MRI task.

2.3.2 Updating the Cortico-Centric Vision

Related to Berridge's first argument, inferences made based on human research, and more specifically neuropsychological testing, have often led to the belief that cognitive impairment is the result of a cortical brain lesion or dysfunction. However, strong evidence is now observed in the literature concerning the role of subcortical structures in a range of highly specialized behavioral functions, including those related to cognition (e.g., Koziol and Budding 2009). Both the basal ganglia and the cerebellum are involved in memory and executive and attentional functions (e.g., Graybiel and Mink 2009; Grahn et al. 2009; Schmahmann 2019; Silveri and Misciagna 2000). Moreover, it has even been shown that during associative learning tasks performed by monkeys in which simultaneous recordings were made in the prefrontal cortex and the caudate nucleus, the activity of the caudate nucleus adapted quickly to contingencies, even before the prefrontal cortex and before a significant improvement in performance occurred (Pasupathy and Miller 2005). This observation suggests that subcortical structures such as the caudate nucleus are likely to be mobilized even before other cortical structures, such as the prefrontal cortex, are mobilized for specific processing and even for high-order controlled cognitive processes. Second, regarding the notion of spatial segregation versus integration, it has been shown that the striatum and cerebellum are also parcellated into functional subdivisions underlying motor, cognitive, and emotional processes (Alexander et al. 1990; Stoodley and Schmahmann 2009). This bias toward cortical activations during emotional tasks performed with brain imaging protocols is more due to the size of the structures, as signal detection does not work in structures whose neurons are too densely packed. In other words, the neurons in subcortical structures, like, for example, in the subthalamic nucleus and hypothalamus, are too closely packed to allow subpopulations to be visualized based on vascular blood flow.

Following this reasoning, we understand why structures that do not belong to the cortex, such as the cerebellum and the basal ganglia, are likely to be involved in the processing of emotions on a sensory as well as a cognitive level. The localizationist vision, used in models to describe brain architecture that supports human emotions, helps conceptualize how an emotional response is generated but does not reflect the complexity of the process, because brain circuits are interconnected at multiple levels and mutually influence each other. Further evidence from neuroimaging and clinical studies suggests a brain network for affective processing—organized in multiple input and output loops that, in addition to the cerebral cortex, include the basal ganglia and cerebellum, in which the three structures are considered "equal functional partners."

2.4 Beyond the Cortico-Centric Bias: The Cerebellum and the Basal Ganglia in the Brain Network Underlying Emotion

Anatomical studies in animals, particularly in studies that use neural tracing techniques, have revealed neuronal connections between the associative areas of the cortex and the basal ganglia, as well as circuits between these same areas of the neocortex and the cerebellum (Bostan and Strick 2010, 2018). Moreover, the structures of the limbic network (e.g., amygdala, cingulate cortex) are connected to the basal ganglia and the cerebellum, which, in addition to the direct connection between these two regions, argues in favor of modulatory and reciprocal influences on affective processing throughout the brain (Habas et al. 2009).

2.4.1 Basal Ganglia Involvement in the Synchronization of Human Emotion Components

Functional MRI studies (Péron et al. 2016), electrophysiological data (Péron et al. 2014; Bénis et al., 2020), and deep brain stimulation (DBS) of the basal ganglia (Péron et al. 2013) have provided direct evidence for a specific role of the basal ganglia in human emotions. Interestingly, researchers have reported deficits in several emotional components following subthalamic nucleus (STN) DBS in patients with Parkinson's disease, allowing a better understanding of the functional roles of the dopaminergic pathways and basal ganglia in these processes. For example, modifications of subjective feeling and arousal have been observed following this surgery (Serranová et al. 2011; Vicente et al. 2009), as well as impairments in both facial (Péron et al. 2010a; Dujardin et al. 2004) and vocal (Péron et al. 2010b, 2015) emotion recognition. Cognitive and action tendency components are also affected, as deficits in inhibition processing (Parsons et al. 2006; Aron and Poldrack 2006) and modulations in motivational processes (Lardeux et al. 2009) were revealed following STN DBS. These results strongly point to the involvement of the STN in all components of emotional processing, leading to a proposal concerning the nature of its role. According to Péron et al. (2013), the STN, together with the basal ganglia, may play a central role in emotional processing by *coordinating the activity* of the cortical and subcortical brain structures needed to process emotions. More specifically, the basal ganglia may retrieve data from different parts of the cortex and subcortex, as well as from the brain stem (Coizet et al. 2009) and the cerebellum (Bostan and Strick 2010), and on this basis, *recruit and synchronize* the activity of the cortical and subcortical structures required for the relevant process. Moreover, the basal ganglia may be critically involved in *constructing performance units of sequence representations*, also called chunks. These packages are composed of specific items of information (e.g., emotional information) previously selected to allow more automatic processing. These chunked patterns occur for sequential, repetitive motor, cognitive, and emotional behaviors (or a combination thereof) induced by a triggered stimulus (internal or external). As result, once started, these behaviors may come to an end without conscious control (Graybiel 2008). Overall, the basal ganglia would play a "meta-role" in emotional processing by selecting and coordinating cortical and subcortical response patterns. The close connections between the basal ganglia and the cerebellum (Bostan and Strick 2018) lead to the question of the intervention of the cerebellum in this hypothesized role of the basal ganglia, as well as the nature of the specific role (if any) that the cerebellum may play in emotional processing.

2.4.2 Cerebellar Involvement in the Synchronization of Human Emotion Components

The hypothesis of cerebellar involvement in emotional processes has been reinforced only in recent years (Adamaszek et al. 2017). Clinical manifestations, such as pathological laughter and crying, or the blunting affect observed in patients with atrophy or cerebellar degeneration or stroke, have prompted researchers to question the role of the cerebellum in human emotions (Kish et al. 1988; Levisohn et al. 2000). Several studies in the literature seem to indicate cerebellar involvement in components of emotional processing.

Subjective Feeling and Arousal Using emotional pictures to induce emotional states, researchers have shown a decrease in pleasant experience in response to happiness-evoking stimuli in patients with cerebellar lesions (Turner et al. 2007) and demonstrated cerebellar activations following the presentation of aversive pictures (Bermpohl et al. 2006). Interestingly, the functional segregation of primary emotions in the cerebellum has been suggested, with spatially distinct patterns of activity in the posterior lobe of the cerebellum, as well as common sites of activation underlying the existence of shared neural networks (Baumann and Mattingley 2012). Moreover, temporal hierarchical processing of arousal and valence has been demonstrated in the cerebellum, with arousal processing first (occurring in both vermal (VI and VIIIa) and hemispheric (left Crus II) lobules) followed by valence processing and its interaction with arousal (occurring in left V and VI lobules and Crus I) (Styliadis et al. 2015).

Recognition of Emotion Studies have highlighted that patients with cerebellar stroke exhibit impairment of facial emotion attribution (Adamaszek et al. 2014), in particular for negative emotions (Moulton et al. 2011; Schutter and van Honk 2009). This disturbance seems not to be specific to the visual modality but is present when emotions are conveyed by the human voice, as there is evidence to support deficits in recognizing emotional prosody (Thomasson et al. 2019; Adamaszek et al. 2014). According to a previous study (Thomasson et al. 2019), fine-grained deficits were observed, with patients giving erroneous ratings on the Surprise scale when they listened to fear stimuli. It seems that the patients identified the target emotion well but, at the same time, made misattributions regarding non-target emotions. Interestingly, these disturbances could be linked with the cerebellar contribution to timing and sensory acquisition (Baumann et al. 2015). Increased cerebellar activity has been reported during pitch discrimination tasks (Petacchi et al. 2011), and in the right cerebellar vermis ($xyz = 2, -64, -34$) which is thought to be related to modulation of fundamental frequency in emotional speech production (Pichon and Kell 2013). Moreover, cerebellar patients have difficulties in comparing the durations of two successive time intervals (Ivry and Keele 1989). More specifically, Gooch et al. (2010) found that patients with damage to the middle-to-superior lobules or the left hemisphere showed more significant impairments in accuracy on several timing tasks, suggesting the specific involvement of these regions in time perception. This therefore suggests early (sensory) but also later (cognitive) cerebellar participation in the processing of emotions, which seems consistent, given the involvement of the cerebellum in cognitive processes.

Appraisal Processes Impairments in executive functions (e.g., set shifting, abstract reasoning, verbal fluency, planning, working memory), often with perseveration, distractibility, or inattention, have been found in patients with cerebellar cognitive affective syndrome (Schmahmann and Sherman 1998). These processes are crucial to emotional processing and their alteration is manifested by disinhibition and poor affect regulation. In addition, recent models include the cerebellum in the decision-making process (Roldan Gerschcovich et al. 2011; Wang et al. 2020), a cognitive function that is largely modulated during the course of an emotional response (Brosch and Sander 2014).

Action Tendencies and Motivational Processes Symptoms such as lack of initiation or apathy could be observed in patients with cerebellar impairment (Schmahmann et al. 2007). Intriguingly, cerebellar dysfunction was found in autism spectrum disorders and schizophrenia (Villanueva 2012), and a disruption in the reward system was shown in patients with these neurodevelopmental diseases (Simon et al. 2015; Dichter et al. 2012). Interestingly, a recent study conducted in mice demonstrated direct excitatory projections from the cerebellum to the ventral tegmental area, which is one of the brain regions that processes and encodes reward. Accordingly, Carta et al. (2019) have suggested that both the cerebellum and the basal ganglia could coordinate dopamine functions and thus regulate the motivation and reward process.

Taken together, this evidence suggests that the cerebellum has a role in all components of emotion. Similar observations have been previously established concerning the STN, it being conceptualized as a structure that would produce temporally organized neural co-activation