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Reward-based learning and emotional habit formation in the cerebellum

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Abstract

There is growing evidence of the cerebellum's contribution to emotion processing from neuroimaging studies of healthy function and clinical studies of cerebellar patients. As demonstrated initially in the motor domain, one of the cerebellum's functions is to construct internal models of an individual's state and make predictions about how future behaviors will impact that state. By utilizing widespread connections with neocortex and subcortical regions such as the basal ganglia, the cerebellum can monitor and modulate precisely timed patterns of events using prediction and reward-based error feedback in a diverse range of tasks including auditory emotion prosody recognition. In coordination with a broader affective network, the cerebellum helps to select and refine emotional responses that are the most rewarded in a particular context, strengthening neural activity in relevant regions to form a representational chunk. This chunked set of affective stimuli, cognitive evaluations, and physiological responses subsequently can be enacted as a unitary response (i.e., an emotional habit) more quickly and with less attentional control than for a novel stimulus or goal-oriented action. Such emotional habits can allow for efficient, automatic, stimulus-triggered responses while maintaining the flexibility to adapt output when prediction errors signal a renewed need for cerebellar modification of cortical activity, or, conversely, may lead to behavioral or mood disorders when habitual responses persist despite negative consequences.

Key-words: cerebellum; basal ganglia; reward; habit; emotional prosody.

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Introduction

The cerebellum’s contribution to motor control has been studied for many decades, yet its role in a broader set of cognitive and affective functions has been emphasized only in the last 20 years (Bostan & Strick, 2018; Buckner, 2013; Schmahmann, 2019). Specifically, as introduced in the earlier chapters of this volume, one area in which the cerebellum exerts its modulatory influence is emotion recognition and expression. Extant findings have demonstrated that as an individual interacts with the environment, the cerebellum constructs an internal model of the current sensorimotor state and predicts how future thoughts or actions will change this state (Ito, 2008; Popa & Ebner, 2019; Wolpert, Miall, & Kawato, 1998). Accordingly, the cerebellum monitors performance via feedback errors, learns rewarded and punished behavioral patterns, and adjusts its functional outputs to optimize neocortical responses. This modulation occurs via reciprocal connections with neocortex and subcortical nuclei that respond to salient, novel, and rewarding stimuli in the environment (Buckner, Krienen, Castellanos, Diaz, & Yeo, 2011; Clausi et al., 2017; Habas, 2018; Hoshi, Tremblay, Feger, Carras, & Strick, 2005; Pierce & Péron, 2020) and allows the cerebellum to contribute to a broad array of tasks.

In order to form an accurate predictive model for such tasks, it has been proposed that the cerebellum participates in sequence learning. This function was first recognized in the motor domain, but now encompasses learning of a diverse set of sequences/patterns based on social cues, verbal or spatial scripts, speech, or emotional stimuli, among others (Ackermann, 2008; Bostan & Strick, 2018; Heleven, van Dun, & Van Overwalle, 2019; Kotz, Kalberlah, Bahlmann, Friederici, & Haynes, 2013; Leggio & Molinari, 2015; Leggio et al., 2008; Peterburs, Blevins, Sheu, & Desmond, 2019; Van Overwalle et al., 2020). By recognizing timing patterns within stimulus sets, the cerebellum, in coordination with the basal ganglia, can predict the subsequent event in a series, biasing reciprocally connected neocortical regions to anticipate and attend to salient or novel features in the environment and prepare motor and cognitive responses (Grandjean, 2020; Péron, Frühholz, Verin, & Grandjean, 2013; Pierce & Péron, 2020; Popa & Ebner, 2019). Over time, predictable sequences or distributed neural patterns are coalesced into mnemonic chunks that can be accessed more readily from memory and executed with minimal top-down control (Graybiel, 2008). The cerebellum thus contributes to habit formation by fine-tuning performance not only in the domain of motor control, but also in the emotional/affective domain (Pierce & Péron, 2020). Habits consist of repetitive motor, cognitive, or emotional behaviors or thoughts elicited by specific stimuli or situations that are learned over time, performed largely automatically without conscious supervision, and are resistant to competing task interference (Graybiel, 2008; Ramnani, 2014); here, we define *emotional* habits as such learned responses that occur in reaction to or via recognition of affective, emotional, or social stimuli and/or involve the performance of repetitive emotional expressions and behaviors. Ideally, emotional habits allow humans to interact effectively with their social peers, moderate their own mental state, adaptively avoid threats, and pursue positive outcomes (Clausi et al., 2017; Grandjean, 2020; Van Overwalle et al., 2020), yet they can also contribute to affective disorders when the habitual behavior is insensitive to contextual cues or negative outcomes. The following sections will provide evidence for the cerebellum's involvement in motor learning and habit formation, describe emotional habit formation using the example of auditory processing of emotional prosody, and finally provide clinical evidence of disrupted affective habit formation and expression in patients with cerebellar damage.

Motor Learning and Rewards in the Cerebellum

Before describing how the cerebellum may support emotional habit formation, it is useful to consider first how the cerebellum supports habit formation and learning in the well-studied motor domain. Indeed, the uniform architecture of the cerebellar hemispheres (but see Apps, 2016) has led researchers to propose that a single computation (or a small set of computations; see Diedrichsen, King, Hernandez-Castillo, Sereno, & Ivry, 2019) accounts for the function of the cerebellum across domains (Schmahmann, 2000). Therefore, the cerebellum is able to participate in a wide range of tasks using a relatively limited set of computations by utilizing topographically organized reciprocal connections with most of the neocortex and a number of subcortical regions (Buckner et al., 2011; Marek et al., 2018; Stoodley & Schmahmann, 2018). The mechanisms underlying learning, rewards, and habit formation have been investigated most thoroughly in the cerebellum with respect to motor function, particularly using animal models that allow for direct and detailed analyses of cerebellar circuitry (Callu, Puget, Faure, Guegan, & El Massioui, 2007; Kostadinov, Beau, Pozo, & Hausser, 2019; Mauk, Li, Khilkevich, & Halverson, 2014). Utilizing these invasive techniques, researchers have characterized the anatomical inputs and outputs of the cerebellum and many of the functional capabilities of its neural circuits, while others have applied these findings to the study of human cerebellar motor function.

Cellular pathways for motor learning

Studies from the animal literature have demonstrated that the cerebellum receives inputs from mossy fibers from the pons and climbing fibers from the inferior olive (Figure 1), which convey different types of information about the individual’s current condition. Mossy fibers transmit signals from the neocortex that correspond to the present sensorimotor and internal state of the individual (Wagner & Luo, 2020). Conversely, climbing fibers convey a teaching signal that is derived from a sensorimotor or reward-based prediction error signal arising from differences between the current and expected state. Manipulation and observation of different cerebellar pathways using the eye blink conditioning paradigm (Freeman, 2015; Hansel, Linden, & D'Angelo, 2001; Mauk et al., 2014) highlighted that the critical contribution of the cerebellum to learning a conditioned response (i.e., a blink after a tone that was initially paired with an air puff) depends upon mossy fiber and climbing fiber signals consistently occurring with optimal temporal proximity (Mauk et al., 2014).

Importantly, the climbing fiber signal shapes how the Purkinje cells, which are the main computational neurons in the cerebellar hemispheres, respond to the numerous granule cell inputs they receive (Hull, 2020; Wagner & Luo, 2020). These teaching signals lead to long term depression of granule cell inputs (parallel fibers) on the inhibitory Purkinje cells, a process which constitutes an important cerebellar learning mechanism (Freeman, 2015; Jörntell & Hansel, 2006), although several complementary mechanisms likely exist across the different neuronal populations of the cerebellum and deep cerebellar nuclei (Hansel et al., 2001; Hull, 2020). Through these synaptic changes, the Purkinje cells learn which granule cells are transmitting pertinent information relative to other contextual signals, thus allowing the cerebellum to improve its computational power, form associative memories, and support adaptive motor control (Ito, 2006). Specifically, cerebellar learning may inform the construction of an internal model of motor movements that represents the current state and expected outcome state, which is shaped iteratively following error feedback and influences the cerebral cortex to optimize behavior as needed (Caligiore et al., 2019; Ito, 2008).

Rewards and motor learning in animals

In addition to the behavioral conditioning paradigms that informed the aforementioned cellular learning mechanisms, learning within the cerebellum also has been demonstrated for reward-based motor paradigms. The reward signals for this type of cerebellar learning may originate from connections with the basal ganglia, including the ventral striatum, and the ventral tegmental area, where dopamine release tracks the positive (reward) or negative (punishment) outcome of a behavior (Bostan, Dum, & Strick, 2010; Carta, Chen, Schott, Dorizan, & Khodakhah, 2019; Hoshi et al., 2005; Hosp et al., 2019; Pelzer et al., 2013). Within the cerebellum, granule cells have been shown to respond to reward delivery and anticipation, as well as to when an unexpected reward is given or an expected reward is withheld (Wagner, Kim, Savall, Schnitzer, & Luo, 2017; Wagner & Luo, 2020). Similarly, climbing fiber input has been shown to convey reward signals in mice performing a visuomotor task, with the strength of the response to predictable rewards decreasing over the course of learning (Kostadinov et al., 2019). This type of diminishing response also was reported in monkeys during reinforcement learning, with the reward-based error signal in Purkinje cells weakening as the animal learned the correct visuomotor association (Sendhilnathan, Semework, Goldberg, & Ipata, 2020). These findings demonstrated that the cerebellum does not calculate a simple motor difference error for specific movements, but that it can account for and receive feedback on reward contingencies and formulate predictions for contextually defined goals.

Human studies of motor and reward-based learning

Extending these findings from animal studies, human neuroimaging studies have shown comparable motor learning activity in the cerebellum. An early functional magnetic resonance imaging (fMRI) study demonstrated cerebellum activation during learning of a sequence of finger movements (Doyon et al., 2002). Participants exhibited cerebellum activation early in the learning process, but this signal diminished after extended task practice and activity shifted to the basal ganglia and neocortex. More recently, Liljeholm and colleagues conducted an fMRI study on habit formation and expression using a novel task designed to distinguish between goal-directed actions and habits (Liljeholm, Dunne, & O'Doherty, 2015). They reported cerebellar and caudate activation primarily for habit learning and response automatization rather than for the implementation of a previously established motor routine. Finally, a study on motor reinforcement learning probed three stages of task performance: exploratory behavior (trial and error), model-based performance, and motor memory-driven responses (Fermin et al., 2016). Along with areas of the prefrontal cortex (PFC) and basal ganglia, the posterior cerebellum was activated for internal model-based learning of response sequences, while the anterior cerebellum was part of a motor network that ultimately stored the memory and implemented the habitual response (see also Penhune & Steele, 2012). Together these studies illustrate that portions of the cerebellum (and basal ganglia) are critical for motor learning as part of a dynamic process of habit formation that shifts from effortful, attention-demanding action exploration to automatic performance of a familiar motor sequence (Ramnani, 2014).

Furthermore, human studies of reward-based learning also have suggested a role for the cerebellum. For example, Ramnani and colleagues conducted an fMRI study in which participants were presented with expected or unexpected rewards and non-rewards, and reported activation in the cerebellar vermis following unexpected rewards (Ramnani, Elliott, Athwal, & Passingham, 2004). Another fMRI study reported left lateral cerebellum activation on trials where participants chose a large, delayed reward over a smaller, immediate reward (Tanaka et al., 2004). These neuroimaging results were followed up by behavioral studies of reinforcement learning that showed faster learning when punishment was administered and better memory when rewards were given (Galea, Mallia, Rothwell, & Diedrichsen, 2015; Song & Smiley-Oyen, 2017). The authors therefore proposed that these feedback methods have different effects on cerebellar error sensitivity, with reward requiring more trials to acquire learning but leading to more lasting effects. Finally, a study of cerebellar patients (Thoma, Bellebaum, Koch, Schwarz, & Daum, 2008) demonstrated that although patients could learn initial stimulus associations successfully, they exhibited deficient reward-based reversal learning. Taken together, these studies suggest that the human cerebellum is involved in reward processing, yet the specific features of the reinforcement learning process to which it uniquely contributes are not fully understood.

Emotional Habit Formation

Based on the findings from motor learning tasks described above and evidence of the cerebellum’s contribution to emotion recognition and expression (Adamaszek et al., 2017; Baumann & Mattingley, 2012; Schmahmann & Sherman, 1998; Strata, 2015; Thomasson et al., 2019; Van Overwalle et al., 2020), it is proposed that the cerebellum performs a similar prediction error-based learning function within the emotion domain and supports the acquisition of emotional habits. When the brain perceives a stimulus and identifies it as biologically relevant (i.e., likely to impact the individual’s homeostatic needs and affective state; Barrett, Mesquita, Ochsner, & Gross, 2007), multiple nodes of emotion, sensorimotor, and cognitive networks are engaged, including the amygdala, basal ganglia, PFC, and cerebellum (Figure 2). The stimulus may consist, for example, of a human voice speaking in a tone and cadence that convey the individual’s emotional state (e.g., a slow, low-pitched voice of a speaker who is sad). This emotional prosody allows individuals to perceive affect from a vocal utterance based on its non-linguistic acoustic properties such as the fundamental frequency (i.e., pitch), energy envelope (i.e., loudness), and timing (Grandjean, 2020; Scherer, 1995). As the brain recognizes the auditory stimulus as salient event, it begins to form an internal representation constructed from the stimulus’ features, its context, prior experience with similar stimuli, possible responses, and likely outcomes (reward or punishment) by strengthening associations between neurons that respond near the time the stimulus occurs, especially when the response yields a positive reward. Over time, a goal-directed behavior for such a stimulus (e.g., approaching someone who is speaking sadly to offer comfort) may shift into a habitual, automatic emotional response (Graybiel, 2008; Liljeholm et al., 2015). The following sections will describe how this emotional representation is constructed and how the cerebellum strengthens and modifies this representation during the habit formation process.

Acquiring emotional “chunks”

Following the initial perception of the stimulus, learning commences as associations form between the acoustic features of the stimulus, visual cues that accompany the voice, the semantic content of the words, and other incidental aspects of the environment (Brosch, Pourtois, & Sander, 2010). A physiological response (e.g., increased heart rate) is paired with preparation for action (e.g., fleeing) and may be tied to a subjective feeling (e.g., fear), which collectively can activate areas including the brainstem, hypothalamus, amygdala, and motor cortex (Aue, Flykt, & Scherer, 2007; Critchley & Harrison, 2013; Sander, Grandjean, & Scherer, 2018; Scherer, 2009). These different aspects of the emotional response then are integrated into a cohesive episode via synchronized long-range neural oscillations that facilitate the transmission of information among sensory, limbic, and cognitive brain regions and allow the emotional experience to reach the level of consciousness (Grandjean, Sander, & Scherer, 2008; Fries, 2005; Péron et al., 2013; Scherer, 2009). Consequently, vocal expressions can be classified as having positive/negative valence, high/low arousal, and/or belonging to a discrete emotion category (Laukka, 2005). The entire experience of the emotional stimulus then is grouped together as a unit or “chunk” that is strengthened through repeated exposure when coupled with positive rewards or the avoidance of punishment. The associated neural pattern of activity can be reactivated automatically during a subsequent encounter to produce the appropriate behavior (Graybiel, 2008; Mauss, Bunge, & Gross, 2007). For example, chunks formed among prosodic sensory cues in superior temporal cortex may be more quickly identified by the PFC as belonging to an angry voice, leading to faster recognition of the social implications of that anger and a better chance of habitually enacting the desired defensive posture or verbal rebuttal (Grandjean, 2020; Pierce & Péron, 2020).

The role of the cerebellum

As other areas of the brain such as auditory temporal cortex, the amygdala, and orbitofrontal cortex begin to analyze the sensory features, salience, and social context of the emotional stimulus, respectively (Grandjean, 2020), the cerebellum monitors the fitness of each element of the response with respect to the current state and goal state, modifying the parameters of the implementation as needed to minimize its prediction error (Leggio & Molinari, 2015; Pierce & Péron, 2020; Schultz & Dickinson, 2000). Additionally, the relative timing of the stimulus components is registered by the cerebellum to build an internal model of the emotional event and its reward (or the lack thereof). As with the motor learning paradigms described above, in the emotional domain, prediction errors conveyed by the climbing fiber signal could shape the sensitivity of Purkinje cells to certain parallel fiber inputs (Wagner & Luo, 2020), strengthening or weakening output signals back to limbic cortical and subcortical regions, such as the orbitofrontal cortex, insula, and amygdala (Buckner et al., 2011; Habas, 2018). If similar stimuli are perceived again at a later moment, the lasting changes in cerebellar synapse sensitivity allow learned neocortical associations to be re-activated more readily and the emotional chunk to be strengthened further when feedback supports the existing model. Over time, this emotional chunk (i.e., pattern of activity in emotion-sensitive regions), or multiple chunks, will be more quickly and automatically selected to generate a habitual response, thereby reducing the need for supervisory posterior cerebellar (and PFC) involvement in habit execution (Doyon et al., 2002; Fermin et al., 2016).

On the other hand, if an unexpected outcome occurs (e.g., mistaking a surprised voice for a fearful voice) that results in a large prediction error from the model (Ito, 2008; Popa & Ebner, 2019), the cerebellum must intervene and instruct downstream neocortical regions to adjust their responses (e.g., firing rates or synaptic weights; Schultz & Dickinson, 2000). In this manner, the cerebellum refines the emotional chunk that was formed in neocortex to better match the emotional stimulus with an appropriate thought or action (e.g., learning that a friend’s surprised (not fearful) voice does not signal a dangerous situation) and minimize the prediction error of its internal model in future encounters. Importantly, learning associations and acquiring habits are dynamic processes in which the cerebellum continually monitors input and output and adjusts the degree of its intervention according to the current context and feedback signals (Caligiore et al., 2019; Peterburs & Desmond, 2016).

In contrast to the posterior cerebellum’s involvement in learning emotional habits, the cerebellar vermis may be especially critical for regulating unconscious autonomic responses to emotional stimuli (Clausi et al., 2017). Indeed, this region often has been identified as a central part of the “limbic cerebellum” in neuroimaging tasks and clinical studies (Baumann & Mattingley, 2012; Colibazzi et al., 2010; Schienle & Scharmuller, 2013; Schmahmann, Weilburg, & Sherman, 2007). The coordination of learning in the associative posterior lateral cerebellum and the automatic physiological response in the cerebellar vermis allows the cerebellum to monitor emotional events and refine behaviors and thoughts to create an optimized habitual emotional response.

Coordination with the basal ganglia

Much of the learning of new habits by the cerebellum occurs with the close cooperation of the basal ganglia (Caligiore et al., 2019; Bostan & Strick, 2018). The basal ganglia work to gate cortical responses to a new stimulus or cognitive state, allowing relevant actions and thoughts to be initiated and inhibiting competing actions/thoughts (Mink, 1996; Nambu, Tokuno, & Takada, 2002). Interestingly, most, if not all, of the nuclei of the basal ganglia contain functional subdivisions that correspond to sensorimotor, associative, and limbic domains, based on their pattern of connectivity with other brain networks (Arsalidou, Duerden, & Taylor, 2013; Krack, Hariz, Baunez, Guridi, & Obeso, 2010; Péron et al., 2013; Pierce & Péron, 2020). These subdivisions are not fully distinct, however, but partially overlap and similar computations may be performed for each functional domain. The dorsal striatum, for example, has been associated with motor habit formation and performance (Packard & Knowlton, 2002). On the other hand, ventral portions of the striatum (including the nucleus accumbens) and the subthalamic nucleus have close connections with limbic regions such as the substantia nigra, amygdala and orbitofrontal cortex and contribute strongly to reward processing and other affective functions such as emotional prosody recognition (Alheid, 2003; Denys et al., 2010; Grandjean, 2020; Graybiel, 2008; Péron, Frühholz, Ceravolo, & Grandjean, 2016). During the formation of emotional habits, processing within the basal ganglia may shift from primarily activating the ventral striatum towards the dorsolateral sensorimotor caudate as behaviors become automated (Yin & Knowlton, 2006). The affective functions of the striatum, thus, influence habit formation in the basal ganglia broadly by signaling which actions yield rewards or punishments in order to strengthen or weaken behaviors associated with a specific stimulus or context (Grahn, Parkinson, & Owen, 2008; Graybiel, 2008; Yin & Knowlton, 2006).

The contribution of the basal ganglia to emotion processing is evident from studies of patients undergoing deep brain stimulation of the subthalamic nucleus to treat motor symptoms in Parkinson's disease, which have demonstrated subtle deficits for both positively and negatively valenced stimuli in both the auditory and visual modality (Drapier et al., 2008; Mallet et al., 2007; Mirdamadi, 2016; Péron et al., 2013; Péron et al., 2010; Péron et al., 2017; Vicente et al., 2009; Voruz et al., 2020). Damage to the basal ganglia, therefore, may disrupt the execution of previously established emotional habits by failing to select the appropriate response and sufficiently inhibit competing responses. As a result, this will have a negative impact on patients' affective functioning without completely eliminating their emotion recognition abilities that rely on other regions such as the amygdala and sensory cortices (Péron et al., 2013).

During healthy emotion processing, the basal ganglia synchronize relevant cortical oscillations by allowing only the correct response to be enacted while inhibiting interference from competing or incidental response activity (Mink, 1996; Péron et al., 2013). This synchronization strengthens a set of events following a given stimulus (i.e., an emotional chunk), building towards a unified representation of the new habitual response (Graybiel, 2008). Once the habit is acquired, less input is required from PFC about current goals or from dopaminergic centers about rewards before a decision threshold is reached and the response can be performed as a complete unit with minimal attentional control. Furthermore, via direct subcortical connections with the cerebellum, the basal ganglia can transmit information regarding the appropriate response, the timing of the response, and reward contingencies of the response to ensure that the cerebellum can update its internal model predictions efficiently (Bostan & Strick, 2018; Buhusi & Meck, 2005; Hoshi et al., 2005; Péron et al., 2017; Pierce & Péron, 2020). As the basal ganglia selects the desired response set, the cerebellum monitors feedback regarding its predictions and continually adjusts activity within the selected (e.g., limbic) regions to improve performance.

Habits and emotional prosody

In the case of emotional prosody, a core cortical network consisting of primary auditory cortex in the temporal lobe, voice sensitive areas in the superior temporal gyrus, and motivation-based evaluative modules in the inferior frontal lobe, responds to the auditory stimulus and extracts relevant affective features. Simultaneously, an extended limbic network that includes the medial frontal lobe, insula, basal ganglia, amygdala, and the cerebellum, modulates the typical response pattern to the stimulus via numerous functional interconnections (Frühholz, Ceravolo, & Grandjean, 2012; Frühholz, Trost, & Kotz, 2016; Grandjean, 2020; Kotz et al., 2013; Schirmer & Kotz, 2006; Witteman, Van Heuven, & Schiller, 2012). The role of the cerebellum (and basal ganglia) in emotional prosody was investigated in a recent fMRI study of healthy adults that utilized pseudosentences spoken by angry, happy, or neutral voices (Ceravolo, Frühholz, Pierce, Grandjean, & Péron, 2021). Portions of cerebellar Crus I and II, lobules VI-VIII, the vermis and the dentate nucleus were more activated when judging angry or happy voices compared to neutral voices and showed heightened functional connectivity with the basal ganglia during the task. These findings indicate that the cerebellum is indeed sensitive to emotional prosody and, more generally, may aid in analyzing non-rhythmic sounds in conjunction with rhythmic sound processing in the dorsal basal ganglia (Breska & Ivry, 2016; Frühholz et al., 2016; Kotz, Stockert, & Schwartze, 2014). Further work is needed to better clarify how the role of the cerebellum in general emotional prosody processing specifically extends to habit formation.

Speculatively, the cerebellum's sensitivity to emotional prosody and temporal patterns may contribute to the emergence of an emotional habit as it builds a prediction for the individual's future sensorimotor and affective state following an emotional auditory stimulus within a certain context (Cheron, Márquez-Ruiz, & Dan, 2016; Ivry & Spencer, 2004). With repeated presentations of this stimulus type, the cerebellum (and other brain regions) begins to learn optimal associations between the inputs and appropriate outputs to create a more structured, automatized response (i.e., a habit) within the cortical regions that process emotional prosody (Grandjean, 2020). Therefore, it is proposed that the cerebellum's demonstrated involvement in emotional prosody processing (Adamaszek et al., 2014; Ceravolo et al., 2021) allows it to construct an emotional habit structure that biases how an individual responds to the next instance of emotional prosody, potentially dampening unproductive physiological responses or elaborating socially meaningful facial cues automatically to communicate most effectively with the speaker.

Clinical Implications

The previous section proposed how emotional habits form in healthy individuals, yet much of the insight into the affective function of the cerebellum originated in clinical studies of patients with cerebellar damage and from anatomical investigations of patients with psychiatric disorders. The disruption of cerebellar function via injury or disease can lead to a myriad of symptoms including affective personality changes and cognitive deficits, in addition to the well-recognized motor dysfunctions (Leggio et al., 2008; Olivito et al., 2018; Schmahmann, 2019; Schmahmann & Sherman, 1998; Turner et al., 2007). These affective changes may arise from improper cerebellar feedback due to inaccurate internal models of emotional contexts that, in turn, disrupt the formation or execution of habitual responses to the emotional stimuli. Differences in cerebellar anatomy and function have been associated with psychiatric conditions such as autism spectrum disorders (ASD), attention deficit/hyperactivity disorder (ADHD), schizophrenia, bipolar disorder, depression, and obsessive-compulsive disorder (OCD; Adamaszek et al., 2017; Anticevic et al., 2014; Bruchhage, Bucci, & Becker, 2018; Chen et al., 2013; Clausi et al., 2019; Depping et al., 2016; Fatemi et al., 2012; Gill & Sillitoe, 2019; Schmahmann et al., 2007), where inappropriate emotional responses may occur or habitual behaviors may persist despite negative affective feedback or punishment. Although each of these conditions involves diverse clinical symptoms and affects numerous brain regions, evidence is accumulating for a specific impact of or on the cerebellum that may alter emotional habit formation and performance.

For example, in OCD and ADHD, problems with impulsive and compulsive behaviors may be due to a difficulty inhibiting motor sequences or interrupting habit performance, processes that normally are supported in part by the cerebellum (Miquel, Nicola, Gil-Miravet, Guarque-Chabrera, & Sanchez-Hernandez, 2019). If the cerebellum cannot accurately construct an internal model, then faulty cerebellar output to PFC or basal ganglia (which may be impaired themselves) can contribute to a failure to select and strengthen the correct response amid competing neural noise, preventing inappropriate or habitual responses from being inhibited and new responses from being learned (Bostan & Strick, 2018; Fermin et al., 2016; Gillan et al., 2011; Gillan et al., 2014; Sander et al., 2018). An inability to incorporate negative feedback for this behavior into a new cerebellar model (perhaps due to disrupted connections with reward systems in the striatum or ventral tegmental area; Bostan et al., 2010; Kostadinov et al., 2019) may perpetuate the undesirable behavior, leading to clinical symptoms. Furthermore, different disorders may reflect disruptions to particular functional loops between the cerebellum, basal ganglia, and neocortex. For example, the persistence of maladaptive habits in OCD may arise from dysfunction within the limbic loop that prevents cerebellar modification to existing habits based on feedback (Miquel et al., 2019), whereas motor (and perhaps affective) symptoms in Parkinson’s disease may arise from deficits in the sensorimotor loop that prevents automatic performance of habits and thus requires increased cerebellar activity to support slow, conscious, executive supervision of actions (Drapier et al., 2008; Péron et al., 2013; Wu & Hallett, 2013).

Furthermore, ASD has been associated with early cerebellar abnormalities, particularly a reduced number of hemispheric (and possibly vermal) Purkinje cells, that may be linked to the development of impaired social/emotional habits in addition to motor and language deficits (Bruchhage, Bucci, & Becker, 2018; Fatemi et al., 2012). For example, difficulties with social skills may arise in part due to affective cues (e.g., an emotional facial expression) that cannot be properly incorporated as feedback signals into an internal model to build predictions and guide the formation of appropriate habitual social responses. Additionally, the repetitive behaviors and preference for routines observed in ASD may reflect altered reward circuitry (Fatemi et al., 2012; Gotham et al., 2013; Subramanian et al., 2017), from which the cerebellum receives input for learning and adjusting behaviors. Nonetheless, the array of ASD symptoms involves numerous mental processes governed by multiple brain regions (such as the basal ganglia) and the precise contribution of the cerebellum has yet to be determined.

More generally, the cerebellum's connections with limbic regions or the default mode network may explain its association with mood disorders and affective symptoms such as neuroticism, blunted affect, or rumination (Clausi et al., 2019; Depping et al., 2016; Lupo et al., 2015; Schmahmann et al., 2007; Schutter, Koolschijn, Peper, & Crone, 2012). Again, the inability to construct accurate models of the current (emotional) state of the individual, their environment and how ongoing (negative) thoughts will impact their mood could lead to inappropriate or inadequate modification of limbic network activity, poor mood awareness (Adamaszek et al., 2017; Clausi et al., 2019), and the persistence of unwanted affective/reward-seeking habits or thought patterns (which may also contribute to drug addiction; Miquel, Gil-Miravet, & Guarque-Chabrera, 2020; Moulton, Elman, Becerra, Goldstein, & Borsook, 2014).

When considering patients with lesions to the cerebellum, one clinical study (Adamaszek et al., 2019) found a higher proportion of errors for emotion recognition (especially fear) for vocal and facial expressions in cerebellar patients with lesions encompassing Crus I and II, as compared to two other patient groups. Their results identified the cerebellum as an important lesion site underlying emotion recognition impairment (see also Thomasson et al., 2019), while patients with dysfunction of the basal ganglia due to Parkinson's disease and patients with general cortical lesions did not show similar deficits, extending their previous findings of emotional impairment in cerebellar patients compared to healthy controls (Adamaszek et al., 2014). These emotion recognition difficulties may have arisen because of the cerebellum's inability to incorporate incoming sensory information (e.g., the emotional prosody of a voice) into its internal model. Thus, when other brain regions such as the PFC and amygdala respond to an emotional stimulus, they may rely upon missing, slow, or faulty cerebellar feedback to adjust the initial prediction for interpreting the perceived emotion, biasing the response towards familiar, habitual emotional reactions with poor specificity to the current context. Despite the current evidence from these various clinical conditions and assessment techniques, the precise causal links between cerebellar anatomy/function and clinical disorders/emotion deficits remain to be clarified fully.

Conclusion

There is increasing recognition across clinical (Adamaszek et al., 2015; Clausi et al., 2019; Leroi et al., 2002; Lupo et al., 2015; Schmahmann & Sherman, 1998; Thomasson et al., 2019; van den Berg, Huitema, Spikman, Luijckx, & de Haan, 2020; Van Overwalle et al., 2020) and neuroimaging studies (An et al., 2018; Baumann & Mattingley, 2012; Bermpohl et al., 2006; Ferrari, Oldrati, Gallucci, Vecchi, & Cattaneo, 2018; Lee et al., 2004; Schutter & van Honk, 2009) of the cerebellum's contribution to non-motor functions, notably in the affective domain. This chapter described findings related to the cerebellum and emotional habit formation, using the example of auditory processing of emotional prosody. The cerebellum builds an internal model of the current state and forms predictions about future states based on the context and one's previous experience with emotional stimuli. Over time, the cerebellum learns associations among stimuli and between stimuli and rewarded responses, and optimizes behavior through outputs to the neocortex and basal ganglia, thus strengthening a repeatedly rewarded response. Once the habit is established, cerebellum involvement is reduced to monitoring for prediction errors while the routine thought or action is completed seemingly automatically. If, however, emotion circuits in the cerebellum are damaged by disease or injury, an individual may present with a mood disorder or dysfunctional reward-seeking behavior, potentially driven in part by the uncorrected implementation of maladaptive emotional habits. In conclusion, although the cerebellum contributes to emotion processing within the context of large, dynamic brain networks, growing evidence indicates that the cerebellum also plays a unique role in processing of prediction errors, rewards, and learning of new habits within the emotional domain.

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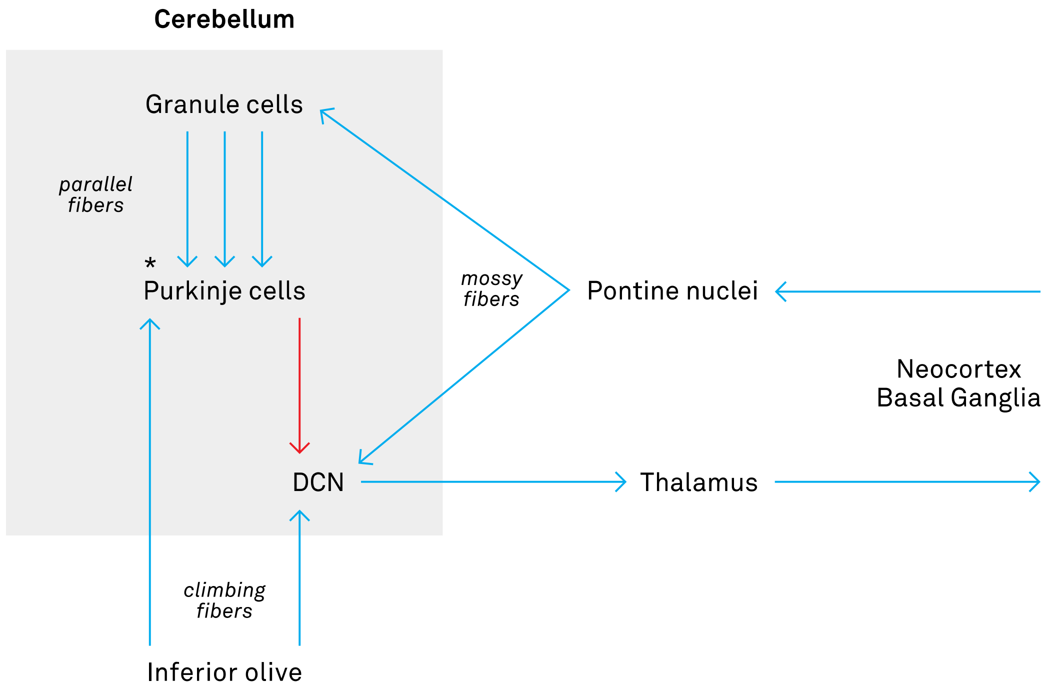

Figure 1. Diagram of the organization of the cerebellum. The figure illustrates the major input/output pathways of the cerebellum and connections within the cerebellum that contribute to prediction error-based learning. Blue arrows denote excitatory connections and the red arrow denotes the inhibitory output from the Purkinje cells. * indicates one site of cellular learning through long term depression. DCN = deep cerebellar nuclei.

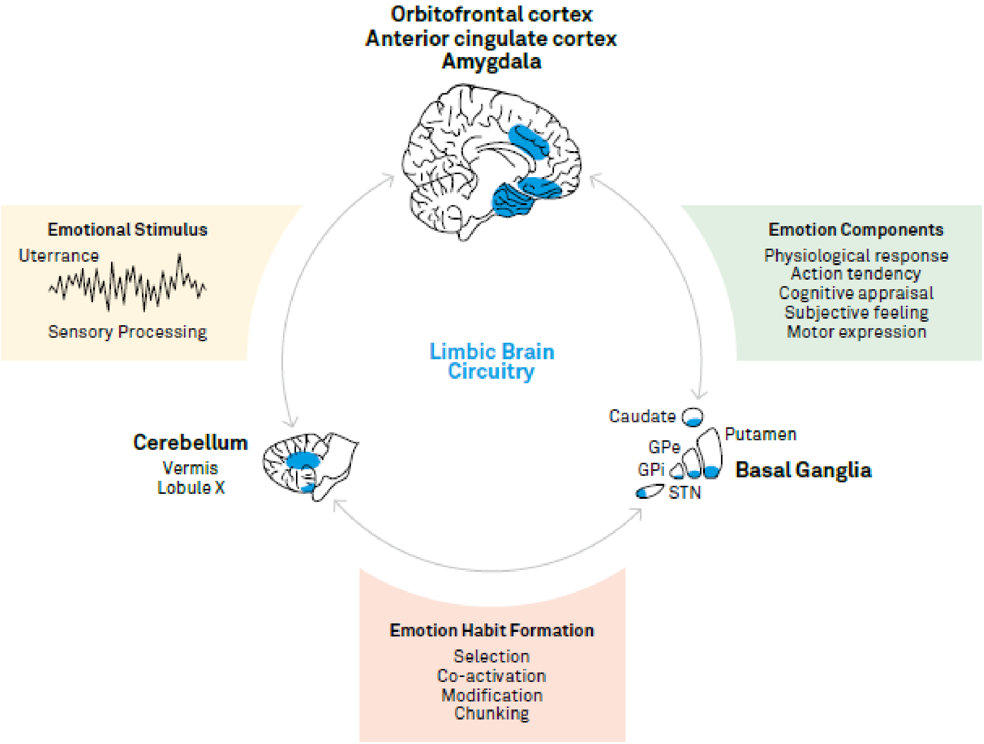

Figure 2. The cerebellum functions as part of a limbic/affective brain network that also includes medial prefrontal/orbitofrontal cortex, the amygdala, and the basal ganglia. Reciprocal anatomical and functional connections between such regions allows the cerebellum to contribute to emotional habit formation by monitoring the internal affective state and fine-tuning output according to prediction and reward-based error feedback signals. In the case of emotional prosody, affective circuitry processes a vocal utterance to extract emotional content and generates components of an emotion experience such as a physiological response, cognitive appraisal, and motor expression. With repeated occurrences of the stimulus, the network iteratively builds towards an emotional habit as selection and co-activation of particular components strengthen their association, forming a “chunk” that can be performed later with minimal attentional control. STN: subthalamic nucleus; GPi: globus pallidus internal segment; GPe: globus pallidus external segment.