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The role of the human cerebellum in performance monitoring

Jutta Peterburs[1,2] and **John E. Desmond**[2]

[1]Institute of Medical Psychology and Systems Neuroscience, University of Münster, Von-Esmarch-Str. 52, 48149 Münster, Germany

[2]Department of Neurology, Division of Cognitive Neuroscience, Johns Hopkins University School of Medicine, Division of Cognitive Neuroscience, Baltimore, Maryland, USA

Abstract

While the cerebellum has traditionally been thought of as mainly involved in motor functions, evidence has been accumulating for cerebellar contributions also to non-motor, cognitive functions. The notion of a cerebellar internal model underlying prediction and processing of sensory events and coordination and fine-tuning of appropriate responses has put the cerebellum right at the interface of motor behavior and cognition. Along these lines, the cerebellum may critically contribute to performance monitoring, a set of cognitive and affective functions underlying adaptive behavior. This review presents and integrates evidence from recent neuroimaging and clinical studies for a cerebellar role in performance monitoring with focus on sensory prediction, error and conflict processing, response inhibition, and feedback learning. Together with evidence for involvement in articulatory monitoring during working memory, these findings suggest monitoring as the cerebellum's overarching function.

Keywords

cerebellum; performance monitoring; cognition; internal model; executive functions

Introduction

The traditional view of the cerebellum as exclusively involved in motor functions has been challenged, amongst other findings, by early reports of cognitive and affective impairments following cerebellar damage [e.g. 1–4], ultimately leading to a fundamental paradigm shift. It is now widely recognized that the cerebellum contributes to motor behavior and cognition, the crucial question being *how* (rather than if) cerebellar involvement in the cognitive domain is implemented (for a review of current theories, see [5]). Anatomically and

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Address for correspondence: Dr. Jutta Peterburs, Institute of Medical Psychology and Systems Neurosciences, University of Muenster, Germany, Phone: +49 251 83 52789, Fax: +49 251 83 55494, Jutta.Peterburs@uni-muenster.de.

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functionally, the cerebellum possesses vast connections to cerebral areas pivotally involved in non-motor functions, and these connections form uniform, closed loops [6, 7]. It has been proposed that these loops may underlie uniform processing habits for the different functional domains [7]. In other words, as the cerebellum is critical for coordination and timing in the motor domain, it may subserve similar functions also in the cognitive domain. Accordingly, motor dysmetria, that is, inability to perform accurate movements due to impaired coordination of the limbs, following cerebellar damage, may be paralleled by “dysmetria of thought” [8] or “cognitive dysmetria” [9], as reflected in affective disturbances, psychotic features and executive dysfunction, depending on the exact location of the cerebellar lesion [10]. In the present review, we will argue that by being right at the interface of motor behavior and cognition, the cerebellum is at an ideal position to crucially contribute to performance monitoring.

Cerebellar internal forward model

The notion of cerebellar internal models [11, 12] underlying prediction and processing of sensory events as well as coordination and fine-tuning of appropriate responses puts the cerebellum at the interface of motor behavior and cognition. Internal models enable diverse aspects of adaptive behavior, e.g. motor learning, maintenance of accurate performance despite feedback delays, and cancelling out of self-generated sensory effects. In the motor domain, forward models integrate current information about the motor effectors, e.g. proprioceptive information about the arm, with efference copies of motor commands e.g. for a reaching motion, yielding an estimate of the consequences of the movement before external feedback information is available [11]. Internal models have been proposed to apply to mental representations and cognition in an analogous manner [12, 13]. Given the importance of cerebellar internal models for adaptive behavior, it stands to reason that the cerebellum critically contributes to performance monitoring.

What is performance monitoring?

Performance monitoring refers to a diverse set of cognitive and affective functions underlying adaptive behavior. In order to adjust our behavior to meet ever-changing demands in a dynamic environment, we need to process (external and internal) performance-related feedback, detect erroneous responses, manage and inhibit conflicting response tendencies, allocate attentional resources accordingly, and regulate emotional responses to specific response outcomes such as rewards or punishment. Generally, performance monitoring is thought to recruit an extensive fronto-striatal network that makes use of dopamine-dependent coding of response outcomes (for a review, see [14]). However, neuroimaging studies have frequently also reported activations within the cerebellum during error processing, reward learning, and reversal learning [e.g. 15, 16], findings that strongly implicate the cerebellum in performance monitoring. Unfortunately, to date, these cerebellar activations have rarely been discussed in detail, so that the exact role of the cerebellum for performance monitoring has remained largely unclear. In the following paragraphs, we will review empirical data for cerebellar involvement in diverse aspects of performance monitoring.

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Cerebellar contributions to sensory prediction

Early research has implicated the cerebellum in sensory acquisition. Activation in the dentate nucleus was observed for both passive and active sensory tasks, that is, for cutaneous stimulation and for tactile discrimination with and without finger movements, but not for finger movements without tactile discrimination [17, 18]. While these findings did not clarify the precise role of the cerebellum in sensory discrimination, they do support the notion that the cerebellum supports the control of sensory acquisition during a range of behaviors, not only motor but also perceptual and cognitive [18].

The cerebellum has since also been strongly implicated in sensorimotor prediction, and here specifically in the cancelling of self-induced sensory stimulation prediction (for a review, see [19]). Activation in the right cerebellar cortex was reduced during a self-generated movement that generated a tactile stimulus as compared to during an identical movement that did not trigger sensory stimulation [20]. These findings show that prediction of movement consequences modulated the cerebellar response. Moreover, cerebellar activation has been shown to contribute to activation decrease in the somatosensory cortex during self-produced tactile stimulation [21]. In the auditory domain, prediction of self-initiated sounds has been linked to suppression of the auditory N100 component in the event-related potential (ERP). In line with cerebellar involvement in sensory prediction, patients with cerebellar damage show largely attenuated or even a lack of N100 suppression [22, 23].

A recent study with event-related functional magnetic resonance imaging (fMRI) has highlighted cerebellar coding of sensory prediction errors [24]. While in the scanner, subjects performed fast out and back reaching movements with a non-magnetic robotic arm that allowed for low friction two-dimensional movements in the horizontal plane. Movements were aimed at visual targets projected onto a back screen that was visible to the participant by means of a mirror. Movements were either aimed at targets which delivered a force pulse if intersected by the movement trajectory, or at a gap between two objects that both delivered force pulses if intersected by the movement trajectory. Missing the target could thus be signaled by either the presence or absence of a force pulse. Interestingly, errors were generally associated with greater activation in “hand areas” in cerebellar lobules V and VI, irrespective of which error signal had been received, indicating that the cerebellum similarly codes prediction errors based on unexpected presence as well as unexpected absence of sensory stimulation.

Prediction not only involves predicting *if* sensory stimulation will happen but also *when* it will occur. A number of studies have addressed cerebellar contributions to temporal prediction. Recently, Avanzino et al. [*25] had subjects predict the end of human body motion (a right hand writing a sentence) and inanimate object motion (a moving circle reaching a target) presented in video sequences that were interrupted by a dark interval while the motion was underway. Specifically, subjects indicated the end of the movement by button press during this dark interval. Inhibitory repetitive 1 Hz transcranial magnetic stimulation (TMS) over the lateral cerebellum immediately before completing the task was associated with increased timing errors for human body motion only, indicating that the

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cerebellum is specifically involved in predicting the consequences of observed motor acts, a cognitive domain tightly linked to the motor system.

Cerebellar internal models code temporal predictability also outside the motor domain. Early investigations by Ivry demonstrated that cerebellar damage also disrupts perceptual aspects of timing [26]. More recently, Kotz, Stockert and Schwartze [*27] investigated auditory deviance processing in cerebellar lesion patients with electroencephalography (EEG) and ERPs. The fronto-central N2b component which has been linked to attentive detection of a deviant tone in a sequence [28] did not differ between patients and healthy controls. In contrast, the P3b, a centro-parietal component associated with updating of mental models [29], was enhanced in controls for deviants in regular sequences. This effect was absent in patients, suggesting impaired processing of temporal predictability of auditory stimuli.

Cerebellar contributions to error processing

Generally, the cerebellum is thought to make rapid predictions about sensory consequences of self-generated movement at very low levels of movement execution, presumably without awareness [19]. Such fast, unconscious predictions crucially depend on efference copies of motor commands. A series of ERP studies with concurrent eye tracking recently showed that damage to the cerebellum is associated with altered processing of saccade-related efference copy signals. Patients with post-acute focal vascular cerebellar lesions showed altered neural responses but intact behavioral performance during saccadic updating, that is, remapping of spatial representations contingent upon saccades [*30,*31]. A post-saccadic positive deflection in the ERP presumably associated with saccadic updating was reduced in cerebellar lesion patients as compared to healthy controls or patients with focal vascular thalamic lesions. A similar pattern was also observed for evaluative saccade processing: Peterburs et al. [**32] reported altered processing of erroneous and correct saccades but preserved performance accuracy in an antisaccade task in cerebellar lesion patients. The error-correct ERP difference waveforms showed reduced amplitudes for patients in the time window of the error-related negativity (ERN) [33] or error negativity [34], an early post-response negative deflection in the ERP associated with error processing that is thought to depend on an efference copy of the motor command for the response [33, 35]. A recent EEG study with patients with progressive cerebellar degeneration complemented these findings [**36]. ERN amplitudes were reduced in patients, and error rates were increased. Voxel-based morphometry (VBM) analysis showed that performance monitoring abnormalities in patients were primarily associated with gray matter volume loss in posterolateral regions of the cerebellar hemispheres. This is consistent with engagement of lateral and inferior cerebellum during response conflict and error processing in a change-signal task [37], and also with a cerebellar functional topography that posits involvement of posterolateral cerebellar regions in complex motor and cognitive functions [38]. Interestingly, a functional magnetic resonance imaging (fMRI) study with Granger Causality Mapping established a causal relationship between cerebellar and ventrolateral prefrontal cortex (vlPFC) activations associated with errors and with post-error slowing in a stop signal task [39]. Results indicated that cerebellar activation directly mediated error and post-error processing in vlPFC via projections to thalamus and supplementary motor area (SMA).

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Cerebellar contributions to feedback processing

In the absence of internal error signals or in complex environments adaptive behavior critically depends on external feedback. In general, the neural systems underlying the processing of feedback and of performance errors largely overlap (for a review, see [14]). Analogous to the response-locked ERN, processing of feedback has been linked to a negative deflection in the ERP that occurs time-locked to feedback presentation, the feedback-related negativity (FRN) [e.g. 40, 41]. Rustemeier et al. [*429] investigated if feedback processing was altered in patients with focal cerebellar lesions using a probabilistic feedback learning task with monetary rewards. Although learning performance was preserved in patients, neural responses were altered, possibly indicating impaired outcome prediction as indexed by an altered FRN. The general result pattern, that is, preserved behavior and altered ERPs, resembles findings for error processing [**32], and may suggest post-acute functional reorganization and compensation in cerebellar lesion patients that presumably is hampered by disease progression in patients with progressive cerebellar degenerative disease [**36]. Alternatively, it has been proposed that cerebellar damage impairs error-based learning while leaving reinforcement mechanisms themselves intact [**43]. In this study, patients with cerebellar degeneration and controls learned a new reaching movement with error-based versus binary reinforcement feedback. Patients varied in reinforcement learning but showed intact retention rates. In contrast, there was a complete lack of error-based learning in patients. Mechanistic modelling of reinforcement learning revealed that learning success depended on a balance of exploration variability and motor noise, the latter being increased in patients, thus reducing the efficacy of reinforcement learning.

Outside the motor domain, evidence for cerebellar involvement in feedback learning has been provided in a study on probabilistic classification learning [**44]. Even though differential coding of positive and negative feedback was not found in the cerebellum in this study, activation in lateral regions (Crus I / lobule VII) increased with higher predictive values of stimulus combinations. It seems conceivable that cerebellar activation during learning of stimuli with high predictive value may reflect formation or updating of an internal model [**44]. In accordance with this notion, cerebellar activations are often reported in studies on probabilistic reversal learning [15, 16]. Reversal tasks present volatile environments which require constant adaptation of response strategies to changing response-reward contingencies. Von der Gablentz et al. [*45] reported lateral posterior cerebellar activations in concert with prefrontal activations for processing of error feedback versus switch feedback in a reversal task. Cerebellar contributions to acquisition and reversal of stimulus-reward representations are further supported by recent findings linking gray matter volume loss in cocaine-dependent subjects in partially overlapping posterolateral cerebellar clusters to both severity of cocaine use (lobule VIII) and to greater reversal costs (lobule VIIb/VIII), that is, larger differences in error rates between trial blocks with original and switched reward contingencies [*46]. While it is difficult to tease apart these two factors, partial rather than full overlap between cocaine use associated regions and reversal learning associated regions appears to suggest that reversal learning deficits are at least partially independent of neurotoxic effects of cocaine [*46].

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Cerebellar activations have also been found during performance of different variants of the Wisconsin Card Sorting Test (WCST) [47], one of the most common tests to assess executive function. In this test, subjects have to match sample cards displaying colored shapes to different reference cards according to specific sorting criteria. Cerebellar activations were particularly pronounced in a task variant in which subjects were not informed about sorting dimensions but instead had to deduce sorting rules from post-response feedback [47]. In line with this, patients who had undergone surgery for removal of tumors affecting the cerebellar hemispheres have been shown to exhibit deficits in set-shifting on the WCST [48]. These findings further emphasize the role of the cerebellum for set-shifting which is critically needed for adaptive behavior.

The studies discussed above all have in common that feedback learning serves the purpose of selecting a motor output or a task response that will most likely be rewarded, thus requiring sensorimotor integration. Interestingly, lateral regions of the cerebellar hemispheres (Crus I and II) have recently also been implicated in feedback learning in a purely cognitive setting. Increased activation in these cerebellar regions was shown in the context of learning of higher order rules which specified the application of second-order rules and thus did not require integration of sensory information with motor effectors [**49].

Cerebellar contributions to response inhibition

Previous work has also explored the role of the cerebellum for response inhibition. An early study with positron emission tomography (PET) reported activation of the cerebellum in a well-controlled Stroop interference task [50]. Classic Stroop tasks require naming of the color of letters spelling a color word (e.g. “blue”) that, when the color word is semantically incongruent with the font color, involves an effortful, conscious response selection process that counteracts an automatic response tendency to read the word. Cerebellar involvement in Stroop performance was supported by findings of impaired color naming with and without interference in patients with recent cerebellar lesions [51]. Interestingly, impaired color naming with interference was also evident at a follow up one year after the lesion event [51].

Brunamonti et al. [*52] tested patients with focal cerebellar lesions with a countermanding task with go-trials requiring responses and stop-trials required withholding of responses. Patients showed increased reaction times on go-trials, especially following errors, and experienced deficits in responding to the stop signal, indicating difficulty in triggering the stop process. Impairment in patients was more severe if the deep cerebellar nuclei were affected. The authors speculated that these results may indicate cerebellar regulation of voluntary actions based on cerebellar influence on the cortico-striatal loop. Evidence to support this claim was recently provided by Picazio, Ponzo and Koch [53]. They showed modulation of functional connectivity between inferior frontal gyrus/left primary motor area M1 and right pre-SMA during response inhibition following repetitive TMS over the right cerebellar hemisphere. Hirose et al. [*54] reported learning-dependent changes in cerebro-cerebellar interactions during response inhibition as revealed by psycho-physical interaction (PPI) analysis. Performance improvement across two sessions of a go/nogo task was accompanied by decreased interaction from the right inferior frontal cortex to the cerebellar lobules VI or VII, while interaction from these cerebellar regions to the primary motor was

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increased. These findings appear to suggest that practice effects are supported by changes in the interplay between posterolateral cerebellum and frontal cortex.

Cerebellar monitoring functions in working memory

Monitoring functions have been ascribed to the cerebellum also outside the classic realm of learning and adaptive behavior. Working memory is one of the cognitive domains most readily associated with cerebellar contributions. Several studies have reported working memory impairment in patients with cerebellar damage [e.g. 55–59]. A growing number of neuroimaging studies have shown robust, load-dependent activations in the cerebellum for working memory [e.g. 60, 61]. Verbal working memory has been linked to discrete activations in superior/lateral (lobule VI, Crus I) and posterior/inferior regions (lobule VIIB/VIIIA) [61–63]. Bilateral superior cerebellar regions are thought to set up a memory trace and maintain it in an articulatory rehearsal loop, while the right inferior cerebellum serves as monitoring region that underlies error-correction by comparing the articulatory trace with representations in a short-term store [61–63, 65]. Along these lines, impaired immediate recall of non-words and impaired rhyme judgments in cerebellar lesion patients have been ascribed to deficient cerebellar-mediated articulatory monitoring [66]. Rhyme judgement and recall of non-words may rely on inner speech to provide input into an articulatory monitoring system that can detect errors in pronunciation. If this monitoring process is deficient, rhyme judgement for words with mismatching orthography and phonology (e.g. consider the rhyme judgement for “fear” vs. “bear”) should be particularly impaired. Consistent with a role for the cerebellum in articulatory monitoring, this result pattern was observed in cerebellar lesion patients [66].

Conclusions

There is a wealth of evidence for cerebellar involvement in performance monitoring, specifically when a motor output is required, but also in cognitive tasks that do not require integration of sensory information with motor effectors. As illustrated in Figure 1, the cerebellum provides a feedforward sensory prediction to prefrontal areas which can then be compared to the actual consequences of an action. The discrepancy between expected and actual consequences creates an error signal that modifies subsequent predictions, thus allowing the cerebellum to achieve performance monitoring functions. We have reviewed evidence for cerebellar contributions to various aspects of performance monitoring such as sensory prediction, error and feedback processing, and response inhibition. Affective aspects of performance monitoring to date remain sparsely investigated, but there is some evidence for a role of the cerebellum in affective processing concerning the subjective perception of regret in a reward/punishment setting [67]. Moreover, lateral posterior cerebellar activations have also been observed in a study on theory of mind and empathy, although these activations were not further discussed [68]. It is conceivable that processes of mentalizing, that is, inferring one’s own and another person’s mental states, and here also self-other discrimination, are linked to affective aspects of performance monitoring. Another line of research posits a crucial role of the cerebellum in articulatory monitoring. Taken together, these findings highlight monitoring as the overarching function of the cerebellum. For systems neuroscience, understanding cerebro-cerebellar interactions is an important step in

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elucidating the complex networks engaged in complex motor and cognitive functions and in predicting and possibly mitigating effects of cerebellar damage on behavior.

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* of special interest

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Highlights

- Cerebellum involved in various aspects of performance monitoring
- Contributions to sensory prediction, error and response conflict processing
- Contributions to response inhibition, feedback learning, articulatory monitoring
- Cerebellum at the interface of motor behavior and cognition
- Monitoring as overarching cerebellar function

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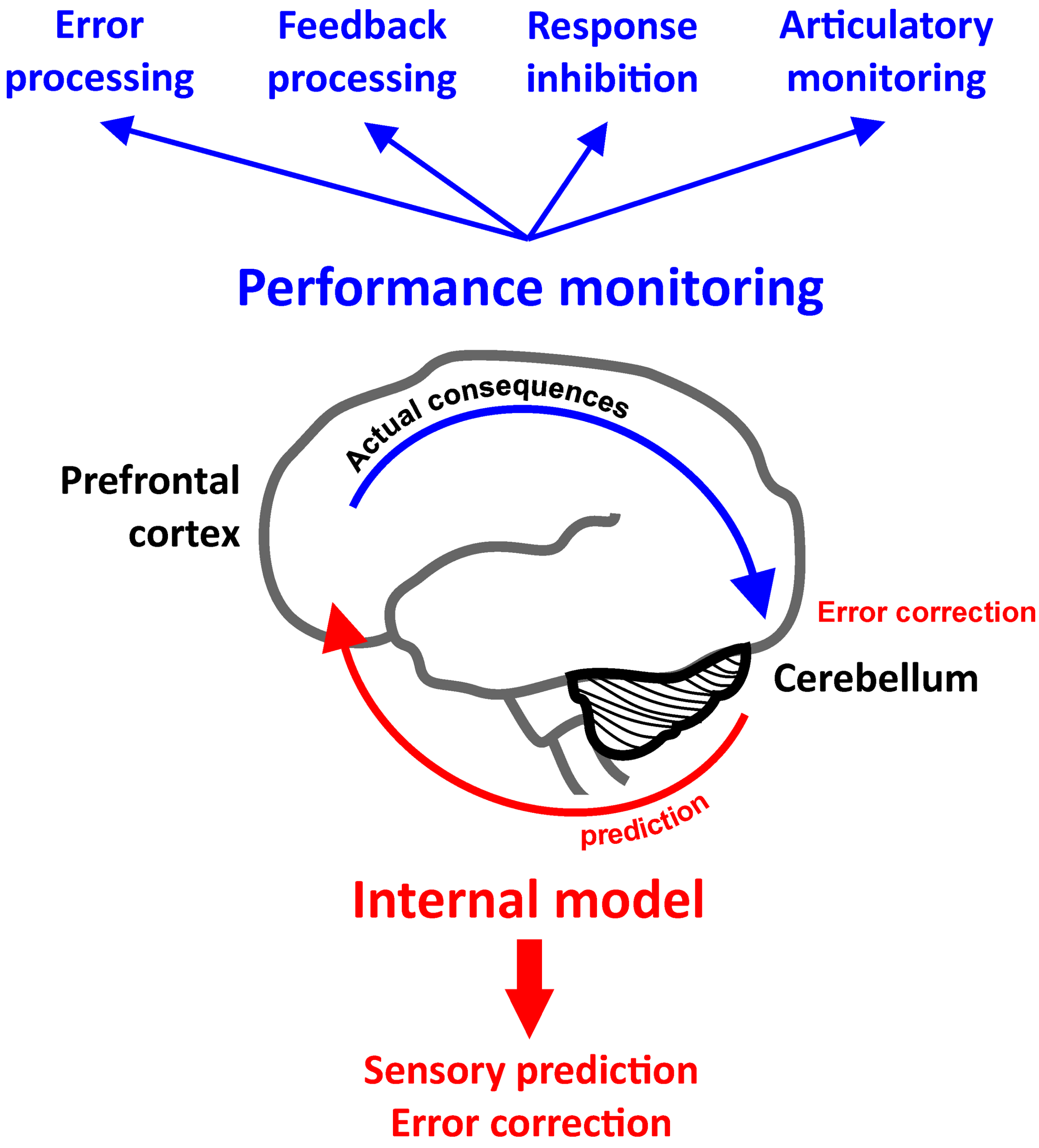

Figure 1.

The cerebellum provides a feedforward sensory prediction to prefrontal areas. A comparison of this prediction with the actual consequences of an action, that is, a discrepancy between expected and actual consequences, creates an error signal that modifies subsequent predictions, thus allowing the cerebellum to achieve performance monitoring functions. In this manner, the cerebellum contributes to higher cognitive functions such as conflict processing, response inhibition, feedback processing, and articulatory monitoring during working memory.

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