Review

Sensorimotor Transformations for Postural Control in the Vermis of the Cerebellum

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The cerebellar vermis plays an essential role in maintaining posture and balance by integrating sensory inputs from multiple modalities to effectively coordinate movement. By transforming convergent sensory information into precise motor commands, it ensures smooth, adaptive motor control, enabling the body to maintain stability in dynamic environments. This review examines recent findings that investigate the distinct neural computations performed by the anterior vermis and posterior vermis (nodulus/ uvula). Specifically, we examine how Purkinje cells in these regions integrate vestibular and proprioceptive signals to convert self-motion information from a head-centered to a body-centered reference frame, which is essential for maintaining precise postural control in response to unexpected movements. Additionally, we consider recent findings showing that, during voluntary self-motion, Purkinje cells in the anterior vermis's role in maintaining balance during voluntary behaviors such as locomotion, its suppression prevents counterproductive stabilizing reflexes, enabling goal-directed movement through space. In contrast, the posterior vermis, encompassing the nodulus and uvula, integrates vestibular inputs from both the otoliths and semicircular canals to maintain equilibrium relative to gravitational forces. We thus hypothesize that Purkinje cells in the nodulus/uvula do not generate suppression signals like those observed in the anterior vermis but instead continuously compute our orientation in space, regardless of whether movement is voluntarily generated or unexpected. If our hypothesis is correct, the nodulus/uvula would effectively provide consistent "ground truth" information about self-motion relative to gravity.

Key words: balance; cerebellum; multisensory integration; proprioception; Purkinje cells; self-motion; vestibular

Significance Statement

The cerebellar vermis is essential for adaptive postural control and motor coordination, transforming sensory inputs into bodycentered motor commands that maintain balance. This review highlights recent findings revealing distinct computational specializations in the anterior vermis and the nodulus/uvula. Both regions integrate vestibular and proprioceptive signals to convert head-centered self-motion into a body-centered reference frame. During voluntary movement, the anterior vermis additionally integrates motor-related inputs to suppress reflexes that would otherwise interfere with goal-directed actions. In contrast, the nodulus/uvula receives direct primary vestibular input but lacks motor input, enabling context-invariant encoding of spatial orientation. We propose that this division of labor supports flexible reflex suppression and stable, gravity-referenced representations—complementary computations essential for maintaining equilibrium in a dynamic environment.

Introduction

The vestibular system detects head motion and orientation relative to space, playing an essential role in self-motion perception as well as generating motor responses that stabilize gaze and posture. Specifically, to maintain postural control, vestibulospinal pathways transmit vestibular information to spinal motor

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neurons. In turn, the motor commands generated by these pathways are essential for stabilizing the body during both voluntary movements and unexpected perturbations, preventing falls and ensuring the smooth coordination of voluntary self-motion (reviewed in Goldberg et al., 2012). Notably, vestibulospinal pathways perform two essential computations to ensure effective postural control during our everyday activities (reviewed in Cullen, 2023). First, they transform the vestibular signals originating from the semicircular canals and otolith organs, which are head-centered, into body-centered and earth-centered reference frames necessary for precise balance and motor coordination. Second, to enable the generation of accurate voluntary movements, the vestibulospinal pathways distinguish between vestibular inputs generated by voluntary self-motion (vestibular

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reafference) versus those arising from unexpected self-motion (vestibular exafference). Specifically, in the case of voluntary movements where the goal is to move relative to space, the stabilizing motor commands produced by the vestibulospinal pathways would be counterproductive, as they would act to resist the intended motion. Thus, it is vital to distinguish between self-generated and external inputs to enable voluntary movement through space (Sullivan et al., 2006; Ilg and Thier, 2008; Kammermeier et al., 2013; Mitoma et al., 2020). Recent work by our group has focused on understanding the key role that the cerebellum plays in these two essential computations.

Damage to the cerebellum results in postural instability, uncoordinated movement, and impairments in both motor learning and balance. Among the regions of the cerebellum, the cerebellar vermis, which is located along the midline, is particularly important for regulating posture and balance (Fig. 1). Notably, the vermis combines sensory input from the vestibular, proprioceptive, and visual systems to control the body's center of mass during both static and dynamic activities. The vermis is functionally divided into anterior and posterior regions that are each thought to make unique contributions to controlling balance via their projections to the most medial of the deep cerebellar nuclei—the fastigial nucleus—as well as the vestibular nuclei of the brainstem (Voogd et al., 1996; Fujita et al., 2020; Gruver et al., 2024).

Lesions in the anterior vermis (Lobules I–V; Fig. 1A, yellow shading) are commonly linked to postural instability and gait ataxia (Diener et al., 1984; Bastian et al., 1998; Sullivan et al., 2006; Ilg and Thier, 2008; Mitoma et al., 2020). Thus, research on this cerebellar region has largely focused on its role in balance and locomotion. Lesions to the nodulus/uvula (Lobules X and IX; Fig. 1A, purple shading) likewise significantly impair posture and balance (Bailey and Cushing, 1925; Mauritz et al., 1979; Diener et al., 1984; Ye et al., 2010). Moreover, these lesions also alter the gravity-related modulation of vestibulo-ocular reflexes (VOR) and optokinetic reflexes (OKR), both of which are essential for maintaining perceptual stability during movement (Voogd and Glickstein, 1998; Angelaki and Hess, 2005). To date, single-

unit recording studies have focused on how nodulus/uvula Purkinje cells integrate vestibular otolith and semicircular canal input to differentiate between tilts and translations—a critical computation for ensuring both postural equilibrium and gravityrelated modulation of VOR and OKR responses (Yakusheva et al., 2007, 2008; Laurens et al., 2013a,b).

Computations in the anterior vermis and nodulus/uvula that transform unexpected vestibular signals from a head-centered to a body-centered reference frame to control posture

Distinct sensorimotor inputs to the anterior vermis versus nodulus/uvula

In order to maintain postural control, it is essential for the brain to compute how the body is moving and oriented relative to gravity to generate robust and appropriate vestibulospinal reflexes, particularly when the consequences of a fall are high (Horslen et al., 2014; Naranjo et al., 2015, 2016). This can be accomplished by integrating proprioceptive input to transform vestibular signals, which are head-centered, into a body-centered reference frame. The outcome of this integration process has been shown by studies demonstrating postural responses evoked by galvanic stimulation of vestibular afferents are modulated by proprioceptive feedback about body position relative to the head (Nashner and Wolfson, 1974; Tokita et al., 1989; Kennedy and Inglis, 2002; Dalton et al., 2017). The anterior vermis and nodulus/uvula are well situated to contribute to this transformation; however, there are some distinctions in their sensorimotor inputs and circuit modules that suggest functional specialization.

In terms of their mossy fiber inputs, Purkinje cells in the anterior vermis and nodulus/uvula are each targeted by brainstem nuclei encoding both vestibular and proprioceptive information, but there are important differences in the sources of these inputs (Fig. 1*A*,*B*). First, while both regions of the vermis receive neck proprioceptive input from the central cervical nucleus (Matsushita and Tanami, 1987), the nodulus/uvula also receives proprioceptive input via the external cuneate nucleus and nucleus *z* (Fig. 1, green arrow; Brodal and Brodal, 1985; Jasmin and Courville, 1987). Thus,



Figure 1. Sensorimotor input to the anterior vermis and nodulus/uvula. Illustration of the input and output of (*A*) the anterior vermis and (*B*) the nodulus/uvula. The anterior vermis receives secondary vestibular input from the vestibular nuclei, neck proprioceptive input from the central cervical nucleus, and motor signals from the motor cortex, lateral reticular nucleus, and basal ganglia. The nodulus/uvula receives input directly from primary vestibular semicircular canal and otolith afferents and proprioceptive input relayed via multiple nuclei (nucleus z, external cuneate nucleus, and central cervical nucleus). Both areas of the vermis provide inhibitory Purkinje cell output to the vestibular and most medial deep cerebellar nucleus (fastigial).

given the projections from multiple nuclei that relay proprioceptive information from the neck and limbs, the nodulus/uvula integrates proprioceptive input from a broader region of the body. Second, while each region of the vermis receives secondary vestibular input from the vestibular nuclei, only the nodulus/uvula receives direct primary afferent input from the semicircular canals and otoliths (Fig. 1, blue arrow; Carleton and Carpenter, 1984). Third, while the anterior vermis receives motor-related signals from the motor cortex, lateral reticular nucleus, and basal ganglia (Fig. 1*A*, red arrow; Wu et al., 1999; Bostan et al., 2010; Coffman et al., 2011), there is, to our knowledge, no known motor-related input to the nodulus/uvula. Finally, there are notable differences in the subnuclei that are the origin of the climbing fibers input to these two regions and, in turn, in the circuit modules formed by their connections with cell groups in the fastigial nucleus (Fujita et al., 2020).

The anterior vermis

The conventional view of the anterior vermis is that it integrates vestibular and proprioceptive signals to generate postural adjustments to compensate for unexpected self-motion and ensure coordinated locomotion (reviewed in Cullen, 2023). Single-unit recording studies in primates have shown that anterior vermis Purkinje cells encode both vestibular and neck proprioceptive information (Manzoni et al., 2004; Zobeiri and Cullen, 2022) and that individual Purkinje cells exhibit substantial heterogeneity in their response dynamics to stimulation of both sensory modalities (Zobeiri and Cullen, 2022). Importantly, the results of our recent experiments have demonstrated how anterior vermis Purkinje cells transform two streams of sensory information into an estimate of body motion. Specifically, these Purkinje cells integrate vestibular and proprioceptive input to encode an intermediate representation of self-motion between head and body motion (Zobeiri and Cullen, 2022). By pooling the activity of a population of anterior vermis Purkinje cells ($N \approx 40$), we could compute representations of both fully transformed body motion and head motion (Zobeiri and Cullen, 2022). Correspondingly, the neurons in the deep cerebellar nuclei targeted by these Purkinje cells fall into these two distinct categories: those encoding body motion and those encoding head motion (Brooks and Cullen, 2009, 2014). Thus, taken together, these findings provide evidence that the integration of vestibular information with neck proprioceptive feedback at the level of the anterior vermis can generate appropriate body-centered postural commands that take into account the head's position relative to the body.

Accordingly, because it integrates proprioceptive information with vestibular signals to transform vestibular input from a headcentered to a body-centered reference frame, it follows that lesions of the anterior vermis result in disrupted postural control. This disruption, in turn, impairs the modulation of vestibulospinal pathways required to accommodate changes in head position (Manzoni et al., 1998; Lam et al., 2016). We further speculate that the convergence of input from a population of Purkinje cells, which each show heterogeneous responses to vestibular and proprioceptive stimulation, provides the necessary flexibility to correct sensorimotor errors and support movement adaptation over time (Sohn et al., 2021). This adaptability likely arises from the diverse response dynamics within the Purkinje cell population, enabling precise recalibration of motor output in response to evolving sensory and motor demands.

The nodulus/uvula

The conventional view is that the primary role of the nodulus/ uvula is to integrate sensory input from the two classes of vestibular organs—the otoliths and semicircular canals (reviewed in

Cullen, 2023). This integration is thought to transform the headcentered self-motion signals encoded by vestibular afferents into earth-centered coordinates to stabilize the head and eyes relative to gravity. Evidence to support this view is provided by studies demonstrating that nodulus/uvula lesions impair the ability to realign the VOR in response to changes in the head's orientation relative to gravity (Angelaki and Hess, 1995; Cohen et al., 1999). Similarly, the nodulus/uvula is important for adapting responses to optokinetic stimulation (reviewed in Barmack and Pettorossi, 2021). Additionally, single-unit recordings from Purkinje cells during unexpected vestibular stimulation induced by wholebody motion have shown that the nodulus/uvula integrates its semicircular canal with otolith afferent input to discriminate head orientation (i.e., tilts) relative to gravity, from linear acceleration (reviewed in Cullen, 2023). This region comprises three distinct groups of Purkinje cells: those encoding tilt, those encoding translation, and in addition a third group that does not differentiate but instead encodes gravitoinertial acceleration, mirroring their otolith afferent input (Yakusheva et al., 2007, 2008, 2010; Laurens et al., 2013a). Its capacity to distinguish between linear acceleration and changes in head orientation relative to gravity underscores the nodulus/uvula's crucial role in computing an accurate internal representation of motion essential for balance and effective navigation.

Although this conventional view of the nodulus/uvula, as reviewed above, highlights its role in integrating semicircular canal and otolith input to stabilize the head and eyes relative to gravity, our recent research has revealed the more expansive role of this region. Importantly, previous clinical studies have shown that damage to this cerebellar region leads to severe balance impairments, such as frequent falls and pronounced oscillations of the head and body (humans, Bailey and Cushing, 1925; Mauritz et al., 1979; Diener et al., 1984; Ye et al., 2010; macaque monkeys, Dow, 1938). Effective balance control relies on the integration of vestibular head motion signals with neck proprioceptive information regarding the relative body organization. Building on this understanding, we hypothesized that this cerebellar region plays a critical role in combining proprioceptive feedback with vestibular signals to generate appropriate compensatory responses for the control of posture and balance. Indeed, we discovered that individual Purkinje cells robustly respond to proprioceptive as well as vestibular stimulation (Mildren et al., 2025). In addition, using computational modeling, we found that pooling the activity of ~40-50 nodulus/uvula Purkinje cells could account for the fully transformed head or body motion representations found in the vestibular and deep cerebellar nuclei (Fig. 2). Notably, as was the case for the anterior vermis, a simple model summing the weighted average activities of a population of nodulus/uvula Purkinje cells during head and/or body motion (illustrated in Fig. 2) is capable of generating the estimate of body motion observed in downstream nuclei neurons. Thus, interestingly, despite the differences in the sensorimotor inputs and circuit modules that suggest functional specialization for the nodulus/uvula versus anterior vermis, the responses of a comparable population of Purkinje cells can achieve similar transformations (Zobeiri and Cullen, 2022).

Taken together, these findings indicate that the nodulus/uvula integrates vestibular information with neck proprioceptive feedback to generate appropriate body-centered postural commands that account for the head's position relative to the body. This finding is consistent with the observation that lesions of the nodulus/uvula have a pronounced impact on postural control (Bailey and Cushing, 1925; Dow, 1938; Mauritz et al., 1979; Diener et al., 1984; Ye et al., 2010), as noted above. Furthermore, given



Figure 2. Pooling responses across a population of Purkinje cells can generate selective head and body motion encoding. Schematic of the convergence of Purkinje cells in the cerebellar cortex onto neurons in the output nuclei (vestibular nuclei, VN; deep cerebellar nuclei, DCN). A population model of the activities of a number of Purkinje cells multiplied by a weighting factor can generate selective head or body motion encoding that is observed in these nuclei neurons during self-motion.

the proprioceptive input from other nuclei, we speculate that the nodulus/uvula may also play a role in transforming vestibular postural reflexes to account for limb organization. Given that the nodulus/uvula also receives proprioceptive input related to limb position, as discussed earlier (Fig. 1), it may further contribute to the transformation of vestibular postural reflexes to ensure coordinated whole-body stability (Allum and Honegger, 1998; Dakin et al., 2013; Forbes et al., 2016). Finally, while our recent results support the primary role of neck proprioceptors, it is possible that cutaneous inputs from the limbs, body, or neck may also contribute to cerebellar activity during motion. For example, during self-motion, inertial forces could modulate mechanoreceptor activity in regions where body mass is supported.

Computational specialization in the anterior vermis versus nodulus/uvula during unexpected self-motion

Overall, there are many similarities in the computations performed across the cerebellar vermis. First, Purkinje cells in the anterior vermis and nodulus/uvula both encode vestibular and neck proprioceptive input robustly (Fig. 3A), with these two modalities summing in a relatively linear manner during concurrent stimulation during head-on-body motion (Fig. 3B). Furthermore, Purkinje cells in both the anterior vermis and nodulus/uvula integrate vestibular and neck proprioceptive input to compute an intermediate representation of head versus body motion (Fig. 3C; Zobeiri and Cullen, 2022; Mildren et al., 2025). Correspondingly, the vestibular responses of Purkinje cells in both the anterior vermis (Zobeiri and Cullen, 2022) and nodulus/uvula (Buron et al., 2023; Mildren et al., 2025) are significantly modulated by the static position of the head relative to the body (i.e., gain fields; Fig. 3D). However, relatively broader tuning is observed in the nodulus/uvula. This modulation in both areas of the vermis is consistent with the observed partial transformation of head-centered vestibular sensory information into the body-centered reference frame necessary for generating appropriate postural reflexes. Finally, pooling across a comparable population size of Purkinje cells, consistent with convergence ratios observed anatomically (Palkovits et al., 1977; Person and Raman, 2012), can explain the body- and head-centered coding (Fig. 3C, green and blue stars) seen in downstream neurons of the rostral fastigial and vestibular nuclei.

However, despite these similarities, there are key differences in how unexpected vestibular and proprioceptive inputs are integrated by these two regions of the cerebellar vermis. Stimulation of the vestibular system versus neck proprioceptors during self-motion typically elicits oppositely directed responses in anterior vermis Purkinje cells (Fig. 3A). This interaction results in a reduced overall response to combined stimulation during head-on-body motion, as the responses to vestibular and proprioceptive stimulation (Fig. 3B, blue and green arrows) effectively cancel each other out. In contrast, Purkinje cells in the nodulus/ uvula agonistically combine these inputs (Fig. 3A,B) such that their responses to vestibular and proprioceptive stimulation (Fig. 3B, black arrow) are effectively enhanced for combined stimulation that occurs during head-on-body motion. We speculate that this synergistic summation in the nodulus/uvula enhances the overall signaling of head motion in space, supporting the vestibulocollic reflex that contributes to the sensorimotor control of head posture across the dynamic motion range experienced during everyday activities (Mildren and Cullen, 2023). Furthermore, the additional proprioceptive input from the limbs, in addition to the neck, may facilitate transforming vestibular head motion signals into appropriate limb postural muscle responses to maintain balance.

Computations that selectively suppress vestibulospinal pathway responses during voluntary self-motion by integrating motor inputs with sensory information in the anterior vermis

During self-motion, it is essential for the brain to distinguish between sensory signals generated by one's own movements and those arising from unexpected perturbations or motor errors. Notably, this distinction allows the brain to correct for unexpected sensory input while also suppressing expected sensory input so as to prevent reflexive muscle activation that would interfere with intended movements, such as navigating through space rather than stabilizing relative to it. The anterior vermis plays a key role in making this distinction. The vestibular responses of its target neurons within the rostral fastigial nucleus and vestibular nuclei that mediate the vestibular spinal pathway are markedly suppressed (by \sim 70–80%) during voluntary relative to unexpected head motion (Fig. 4; Brooks and Cullen, 2009; Brooks et al.,



Figure 3. Integration of vestibular and proprioceptive input in the vermis. *A*, Schematic of responses of an anterior vermis and a nodulus/uvula Purkinje cell to vestibular stimulation (wholebody motion) and neck proprioceptive stimulation (body-under-head motion). Head and body velocity are shown in the top row, with the Purkinje cell simple spike firing rate (gray-shaded area) below. *B*, Schematic of an anterior vermis Purkinje cell showing responses that tend to summate vestibular (blue arrow) and proprioceptive (green arrow) signals antagonistically, leading to smaller responses to combined stimulation (black arrow). In contrast, nodulus/uvula Purkinje cells tend to sum these inputs synergistically, leading to the enhanced response to combined stimulation shown in this example schematic of a nodulus/uvula Purkinje cell. *C*, Spread of head and body sensitivity ratios for anterior vermis and nodulus/uvula Purkinje cells, in comparison with pure head-centered (blue star) and body-centered (green star) motion coding. *D*, Comparison of the mean tuning curves of vestibular responses during different head-on-body positions in the anterior vermis (yellow line) versus nodulus/uvula (purple line).

2015), whereas vestibular afferents encode both classes of stimuli in a context-independent manner (Cullen and Minor, 2002; Sadeghi et al., 2007; Jamali et al., 2009; Mackrous et al., 2022). Furthermore, this cancellation only occurs in conditions where there is a match between the proprioceptive feedback that is experienced and that expected based on the motor command that was generated (Fig. 4; Roy and Cullen, 2004; Brooks and Cullen, 2014; Brooks et al., 2015). Together these results have established that the brain builds an "internal model" of the expected sensory consequences of its voluntary motor commands.

To determine the source of the internal model underlying the cancellation of vestibular reafference, we recently completed a series of recording experiments in the rhesus monkey anterior vermis. It was initially hypothesized that individual Purkinje cells would exhibit stronger modulation during active movement, thereby increasing their inhibitory output to more effectively suppress incoming vestibular input to vestibular or deep cerebellar nuclei neurons. Surprisingly, however, we found that individual anterior vermis Purkinje cells—which, as reviewed above, robustly encode unexpected self-motion (Fig. 3A)—generally exhibited reduced activity during voluntarily generated movements (Zobeiri and Cullen, 2024). We further found that when monkeys attempted to generate head motion relative to space but were unable to do so due to experimentally imposed

movement restrictions, anterior vermis Purkinje cells displayed clear motor-related responses. Thus, these findings suggest that the overall response during voluntary movement reflects the integration of motor-related signals (Fig. 5, red mossy fiber inputs) with vestibular and proprioceptive inputs (Fig. 5, blue and green mossy fiber inputs), where each neuron's lower sensitivity to predictable voluntary motion—compared with unexpected selfmotion—results from combining motor information with sensory input.

Despite this counterintuitive finding that simple spike modulation decreases rather than increases during active movement, we have shown, using a simple linear computational model, that an effective predictive suppression signal can be computed as a result of the diversity of responses observed across the anterior vermis Purkinje cell population. Notably, this population includes both Type 1 Purkinje cells (Fig. 5., Purkinje cell 1), which increase their firing during passive ipsilateral motion, and Type 2 cells (Fig. 5, Purkinje cells 2 and 3), which decrease their firing. During passive motion, the opposing responses of these two types can offset one another, resulting in little net change in inhibitory output and, consequently, minimal suppression of sensory input to downstream pathways. This concept is illustrated schematically in Figure 5. In contrast, during voluntary movement, the integration of motor command signals that selectively attenuate the modulation of Type 2 neurons functions to effectively shift the population balance, increasing net inhibitory output and thereby enabling reafference suppression.

While a uniform increase in Purkinje cell firing might intuitively appear to offer a more straightforward mechanism for



Figure 4. Model of the suppression of self-generated vestibular feedback during voluntary movement. Based on voluntary motor commands, the cerebellum generates a forward internal model of the predicted sensory consequences of the intended movement. If the actual proprioceptive feedback matches this prediction, a cancellation signal is sent to suppress self-generated (reafferent) vestibular sensory feedback that would generate postural reflexes via the vestibulospinal reflex pathway that could interfere with the intended movement. (VN, vestibular nuclei; DCN, deep cerebellar nuclei).

cancellation, we speculate that such a strategy would incur greater metabolic costs due to the energetic demands of maintaining elevated firing rates across the population. Instead, the cerebellum appears to leverage heterogeneity in Purkinje cell responses to achieve suppression efficiently. Overall, we found that a model incorporating the responses of ~40 Purkinje cells could accurately predict the sensory consequences of voluntary movements-to account for the sensory cancellation observed in early vestibular pathways (Zobeiri and Cullen, 2024). Taken together, these findings suggest that cerebellar Purkinje cells combine sensory and motor information to construct the internal model of the sensory consequences of active self-motion in macaques required for cancellation of reafference (Fig. 4). Elucidating how the cerebellum learns to appropriately weight these diverse Purkinje cell responses to achieve such precise cancellation represents an important direction for future research. In this context, the anterior vermis offers a well-characterized system for probing the plasticity mechanisms that enable flexible and adaptive motor control throughout development.

Future studies: computations in the nodulus/uvula during voluntary self-motion

As reviewed in the section above, our recent studies establish that the anterior vermis of the cerebellum plays a key role in generating internal models that predict the sensory consequences of self-generated movements. This raises the question: does the cerebellum also unambiguously track the organization of the head and body relative to gravity during both unexpected and voluntary motion? When navigating the world or changing orientation relative to gravity, accurate tracking of total orientation and motion is essential for functions such as navigation, postural control, and autonomic regulation. For instance, changes in



Figure 5. Mechanisms underlying reafference cancellation by anterior vermis Purkinje cells. Schematic of vestibular, proprioceptive, and motor input to the cerebellar cortex via mossy fiber input to granule cells, which provide parallel fiber input to Purkinje cells. The combination of these sensorimotor inputs from mossy fibers generates distinct Purkinje cell simple spike responses during passive (blue line) relative to active (red line) motion. The summation of responses across heterogeneous Purkinje cells—for example, Purkinje cells 1–3—can generate cancellation signals required to suppress incoming vestibular input to nuclei neurons to suppress vestibulospinal reflex output to ascending and descending pathways.



Figure 6. Self-motion computations performed in the vermis. *A*, Schematic of an example response of an anterior vermis Purkinje cell to unexpected versus voluntary head motion and hypothesized responses of a nodulus/uvula Purkinje cell to voluntary head motion. Nodulus/uvula Purkinje cells may show either a suppression of voluntarily generated sensory feedback (hypothesis 1) or unaltered encoding of voluntary head movement relative to unexpected motion (hypothesis 2). *B*, By combining secondary vestibular, proprioceptive, and motor input, the anterior vermis computes only unexpected motion of the head and the body in head coordinates. From vestibular (including semicircular canal and otolith primary afferent input) and proprioceptive input, we propose that the nodulus/uvula computes total (voluntary and unexpected) head and body motion in earth coordinates.

center of mass location resulting from a translation or tilt, whether voluntarily or externally induced, necessitate adjustments in antigravity muscle activity to maintain balance.

It has been assumed that the nodulus/uvula, like the anterior vermis, implements forward internal models to suppress voluntarily generated vestibular feedback (Laurens, 2022; Fig. 6A, hypothesis 1, red line). However, there are reasons to question this assumption. First, unlike the anterior vermis, to our knowledge the nodulus/uvula lacks motor inputs to compute sensory consequences of self-generated actions. Second, the nodulus/ uvula uniquely receives substantial direct input from both semicircular canal and otolith primary vestibular afferents, which faithfully encode head motion in all contexts (Cullen and Minor, 2002; Sadeghi et al., 2007; Jamali et al., 2009; Mackrous et al., 2022). This veridical feedback about head motion is transmitted to cerebellar granule cells in the nodulus/uvula as excitatory mossy fiber inputs. Third, Purkinje cell output from the nodulus/uvula projects to distinct fastigial nucleus regions, separate from the anterior vermis, which in turn contribute to diverse functions such as spatial memory, arousal, and autonomic regulation (Dietrichs, 1983; Bernard, 1987; Ikeda et al., 1989; Fujita et al., 2020).

Based on these considerations, we hypothesize that the nodulus/uvula does not generate suppression signals like the anterior vermis. Instead, we speculate that it similarly computes self-motion and spatial orientation, irrespective of whether movement is voluntary or unexpected (Fig. 6A, hypothesis 2, purple line). Testing these hypotheses will require recording nodulus/uvula Purkinje cell activity during unrestrained voluntary head movements. Importantly, linear translations stimulate the otoliths, while tilts stimulate both the semicircular canals (via angular motion) and otoliths (via changes in gravitational orientation). We speculate that both tilt and translation will be encoded with equal accuracy during voluntary and unexpected motion. Consequently, the nodulus/uvula would provide precise head and body motion and orientation signals to specific ascending and descending pathways, contributing to functions that could benefit from unambiguous coding of motion and orientation (e.g., spatial memory, arousal, autonomic regulation; Starr and Summerhayes, 1983; Cornwall et al., 1990; Goto et al., 2001).

Conclusion

In summary, the cerebellar vermis plays a fundamental role in integrating vestibular and proprioceptive inputs to stabilize posture and maintain balance, which are essential to support coordinated movement. Our recent findings establish that the anterior vermis integrates sensory and motor-related information to generate internal models that predict sensory consequences of voluntary self-motion, selectively suppressing vestibulospinal pathway responses to enable goal-directed movement. Thus, the integration of motor, secondary vestibular otolith and semicircular canal, and neck proprioceptive input enables the anterior vermis to compute unexpected head and body motion (Fig. 6B). Conversely, the posterior vermis, particularly the nodulus/uvula, integrates indirect and direct otolith and semicircular canal vestibular input, along with proprioceptive input, to compute head and body motion in earth-centered coordinates (Fig. 6B, bottom panel). Future studies are necessary to understand how the cerebellum achieves the appropriate drive to downstream nuclei neurons at the level of its intrinsic circuitry and how it can shape this drive based on its inherent plasticity in everyday life. In addition, investigations into nodulus/uvula Purkinje cell activity during voluntary movement will provide critical insights into its role in generating precise, unambiguous self-motion signals, thereby advancing our understanding of cerebellar contributions to spatial orientation and balance.

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