Cortico-cerebellar interactions during goal-directed behavior

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Summary

Preparatory activity is observed across multiple interconnected brain regions prior to goal-directed movement. Preparatory activity reflects discrete activity states representing specific future actions. It is unclear how this activity is mediated by multi-regional interactions. Recent evidence suggests that the cerebellum, classically associated with fine motor control, contributes to preparatory activity in the neocortex. We review recent advances and offer perspective on the function of cortico-cerebellar interactions during goal-directed behavior. We propose that the cerebellum learns to facilitate transitions between neocortical activity states. Transitions between activity states enable flexible and appropriately timed behavioral responses.

Highlight

- Preparatory activity reflects activity states representing specific actions
- Preparatory activity is dependent on cortico-cerebellar interactions
- The cerebellum learns to use one neocortical activity state to drive the next
- Transitions between activity states enable flexible and appropriate actions

Introduction

Neocortex is critical for adaptive, learned goal-directed behavior. Complex neural activity dynamics in the neocortex reflect the integration of external and internal information prior to selecting and executing specific actions or choices. Neocortex sends long range projections to all major subcortical motor areas, including the basal ganglia, midbrain, and the cerebellum [1-4]. In turn, the outputs of these subcortical structures primarily *converge* in the thalamic nuclei that target areas of the neocortex involved in movement planning and execution. What could be the function of these elaborate cortico-subcortical loops?

Here we offer a perspective on the interactions between neocortex and the cerebellum during goal-directed movements. The cerebellum is classically thought to be involved in motor control. Recent evidence suggests that the cerebellar function is more expansive [5-7], including reward prediction [8-12], motor planning [13-16], and navigation [17]. New advances in neurophysiological methods and behavioral paradigms in rodents now allow a closer examination of cortico-cerebellar interactions during complex sensorimotor tasks.

The same basic circuit structure is repeated across the cerebellum. This has led to the idea that the cerebellum may control activity in other parts of the brain in ways analogous to how the cerebellum controls motor effectors [18]. During motor control, the cerebellum uses efference copy of the motor commands to generate predictive signals that help steer movement toward desired endpoints [19,20]. In this review, we synthesise recent work on cerebellar and neocortical dynamics, and propose that goal-directed movement is prepared by steering neocortical dynamics into specific activity states representing specific future actions. The cerebellum learns to use one pattern of neocortical activity to enable the next, thus steering transitions between activity states (Fig 1). Transitions between activity states enable flexible and appropriate motor plans or response sequences. The same principles may broadly apply to cerebellar contribution towards neocortical computations during other non-motor cognitive behaviors.

Activity states in motor cortex represent upcoming actions

Frontal and motor areas of the neocortex are required for selecting appropriate goal-directed movements. For the purpose of this review, we define motor cortex as regions of the neocortex that have been implicated in motor planning and execution, encompassing areas elsewhere referred to as primary motor cortex, secondary motor cortex, premotor cortex, and anterior lateral motor cortex. Motor cortex neurons become active hundreds of milliseconds before movement onset [14,21-26]. Preparatory activity is best understood as a population response. In activity space, where individual dimensions are the firing rates of

individual neurons, preparatory activity is represented as trajectories that converge onto discrete locations in activity space [27,28]. The process of motor planning can be described as bringing neocortical activity into specific endpoints in activity space. Trajectories describe transitions between neocortical activity states, with different trajectory endpoints corresponding to different future movements or movement plans (Fig 2A).

Recent perturbation experiments have begun to establish a causal relationship between these endpoints in activity space and subsequent movements. For example, when activity trajectories are close to these endpoints, subsequent movement initiation is faster. When preparatory activity is pushed away from the endpoints by perturbations of neural activity, the reaction time is increased [29]. When activity is experimentally pushed to another endpoint, a different subsequent movement results, predicted by the perturbed dynamics [30,31] (Fig 2A). Thus, these endpoints represent internal activity states that specify upcoming movements, without triggering the movements [32,33]. Preparatory activity trajectories are thought to be limited to dimensions of activity space that are orthogonal to dimensions that drive downstream motor centers (output-potent) [32]. Once the endpoints are reached, the corresponding movement can be readily triggered by a separate movement initiation signal [34], which initiates the activity dynamics along the output-potent dimensions.

In theories of motor control, sensory feedback or unexpected perturbations do not trigger immediate motor response [35], but are integrated with the current motor state and intended movement goals to generate appropriate behavioral output [36-38]. The internal activity states that specify future movements without triggering the movement may serve intermediary roles that decouple incoming sensory input from premature motor output in order to enable flexible responses in a particular context. A recent study examined mice navigating a visual virtual reality in which the corridor sometimes changed direction unexpectedly. Motor cortex activity was necessary for corrective turns induced by the unexpected visual perturbation. In contrast, spontaneous turns were independent of motor cortex activity [39]. Conceptually similar experiments were also carried out in non-human primates during visually-guided arm movements [40]. Unexpected sensory perturbations induced activity changes in motor cortex, but the activity was initially orthogonal to dimensions of activity space that control movement. This created a brief 'buffer' decoupling the motor cortex output from the immediate sensory feedback activity, which later could reshape activity dimensions controlling movement to produce appropriate corrections [40,41]. These findings suggest that unexpected sensory feedback can rapidly reshape neocortical activity states representing upcoming movements and consequently generate appropriate motor responses. Consistent with this idea, lesions of the motor cortex in rats compromise their ability to respond to unexpected perturbations [42]. Optogenetic suppression of motor cortex impairs mice's ability to make corrective movements [43].

Motor cortex dynamics transitioning between activity states representing different movements (prior to movement) likely mediate adaptive responses to sensory inputs and unexpected perturbations of sensory context.

Cortico-cerebellar loops in motor planning

How motor cortex dynamics map sensory input and perturbations onto appropriate activity states corresponding to specific actions remains unclear. In the dynamical systems view [27], motor cortex activity unfolds from current activity state into future activity states governed by intrinsic dynamics and external input. We propose that the cortico-cerebellar loop may be part of the same dynamic system that mediates the unfolding of activity dynamics during motor planning. We further propose that the cerebellar input could steer transitions between neocortical activity states, where it uses one pattern of activity to drive the next. The motor cortex sends a copy of its activity state to the cerebellum through the pontine nucleus and cerebellar feedback influence motor cortex activity through the thalamus (Fig 1B) [44]. Several recent studies show that the cortico-cerebellar loop propagates activity related to sensory, motor, and anticipatory signals before an upcoming movement [8,13-15,45].

The anterior lateral motor cortex (ALM) in the mouse is critical for motor planning and movement initiation [46-48]. Chabrol et al examined ALM and cerebellar activity in mice navigating a virtual reality. Mice received rewards at a particular location in the corridor indicated by visual landmarks. Mice learned to decelerate pre-emptively at the anticipated reward location and licked for reward. Long before mice stopped running, neurons in both ALM and cerebellar nuclei exhibited anticipatory activity that predicted the stop [14] (Fig 2B). In a conceptually similar experiment, Gao et al examined head-restrained mice performing a delayed response task in which they reported a tactile decision by directional licking. Preparatory activity predicting the upcoming licking direction was observed in both ALM and cerebellar nuclei [15] (Fig 2C). Furthermore, Wagner et al performed 2-photon calcium imaging in head-restrained mice performing a forelimb reaching task, correlated preparatory activity was observed in the rostral forelimb area (which overlaps with ALM) and cerebellar granule cells [8,13]. These results in rodents mirror those in non-human primates, where cerebellar output neurons exhibit ramping activity predictive of the timing and direction of self-initiated saccades [49-51]. Similar ramping before a saccade has also been observed in the motor thalamus [52] and motor cortex [53-55].

It is important to caution that some of the anticipatory activity might reflect reafferent signals from ongoing movements preceding a reward [56] or preparatory postural adjustments [57], which are not always measured in experiments. At the same time,

cognitive signals within the motor system related to decision-making and motor planning could also be reflected in downstream motor effectors [58]. Within the tightly coupled sensorimotor loops, it remains to be determined which brain structures and specific activity dynamics causally contribute to preparatory activity that influences future behavior.

Recent studies have begun to use activity manipulation experiments to assess the causal contributions of motor cortex and the cerebellum to preparatory activity. These experiments show that preparatory activity in motor cortex and the cerebellum depends on each other. Preparatory activity observed across all three cerebellar nuclei [14,15] is abolished when inactivating ALM [15]. Consistent with motor cortex influencing cerebellar activity through the pontine nucleus during motor planning, inactivation of the pontine nucleus reduces correlated preparatory activity in motor cortex and cerebellar granule cells [13]. Conversely, optogenetic manipulation experiments show that the cerebellum influences the motor cortex by influencing the thalamus. Two studies found that preparatory activity in ALM was abolished by silencing the cerebellar nuclei [14,15] (Fig 2B-C). These findings suggest that the motor cortex and cerebellum work together to generate or maintain preparatory activity.

The cerebellum mediates transitions between neocortical activity states

Beyond demonstrating its necessity, these studies left unclear what specific function the cortico-cerebellar loop serves during motor planning. The theory of cerebellar function proposed by Marr and Albus [59-61] suggests that the cerebellum performs predictions guided by supervised learning [62,63]. The granule cells preprocess the mossy fiber input arriving from the pons into a basis set suitable for supervised learning [5,63,64]. More specifically, this preprocessing breaks the input stream into bits of features which are also dispersed over hundreds of milliseconds [65,66], where specific parts of the input can be associated to produce appropriate output patterns in Purkinje cells, the sole output neurons of the cerebellar cortex. Purkinje cell responses can be adjusted through a well-described plasticity mechanism, whereby a teaching signal (an error signal) provided by the climbing fibers instructs the association of Purkinje cell input [59-61]. The objective function of the cerebellum is therefore to minimize the error signal in climbing fibers by reweighting the inputs [63,65,67,68]. Once learned, the Purkinje cells can generate predictive signals that are triggered by inputs to minimize future errors. In this manner, the cerebellum can use one input activity pattern to enable the next [69]. Cerebellar inputs could be related to external sensory stimuli [65,68,70], internal signals such as efference copies of motor commands [20,71] or persistent activity associated with working memory [72,73].

This general function of the cerebellum may not only adjust movements, but could also influence activity in any region of the brain that is reciprocally connected with the

cerebellum. The anatomical arrangement of the cortico-cerebellar loop provides a rich substrate for multiplexing of diverse representations and feedback control. The pyramidal tract-type neurons from the entire neocortex send collaterals into the pontine nucleus [4,74,75] that gives rise to diffuse mossy fiber input to the cerebellum [76-78]. The neocortical input activity therefore may represent sensory, motor, or internal signals, permitting the cerebellum to associate diverse contextual input with specific reward or teaching signals *via* the climbing fibers to shape output activity in the cerebellar nuclei. The cerebellar nuclei in turn can exert specific influences on the thalamus and motor cortex, and influence the neocortical activity into activity states corresponding to future actions appropriate for a given context. Transitions between activity states could be learned by plasticity mechanisms within the cerebellum (see below) and could be triggered by neocortical input activity related to sensory stimulus, current motor state, or unexpected perturbations. Thus, the cerebellum may steer the neocortical dynamics to enable an upcoming rewarding action, flexibly switch between different actions, or compensate for unexpected perturbations.

Dimension-specific interactions

Action-related information is coded in dynamics along specific dimensions in activity space [32,79]. In specific tasks, only activity dynamics along specific dimensions predict upcoming movements ("coding dimension"), while activity along other dimensions appears to have little influence on behavioral output [30,32,79,80]. Moreover, each task requires representation of a unique set of behavioural variables (e.g. choice, value, timing, etc.), which could be mapped onto different dimensions of population activity in the neocortex [81]. The cerebellar outputs are channeled through distinct cerebellar nuclei, which targets different but overlapping parts of the thalamus [15,82] (Fig 3), forming parallel cortico-cerebellar loops [44]. Distinct cortico-cerebellar loops may influence activity in overlapping swathes of motor cortex. We propose that distinct cortico-cerebellar loops may selectively influence motor cortex activity along subsets of dimensions (Fig 3). The influence of cerebellar feedback onto specific dimensions of neocortical activity may be established through learning. Each cortico-cerebellar loop may initially influence activity in multiple dimensions, and its influence along certain dimensions could be selectively reinforced by cerebellum-dependent supervised learning. Dimension-specific communication [83] may allow different cerebellar nuclei to differentially influence activity in motor cortex related to different actions.

Consistent with this idea, a recent study by Gao et al examined the influence of fastigial and dentate activity on ALM dynamics related to motor planning of directional tongue movement [15]. Both fastigial and dentate perturbations produced activity changes in ALM. Interestingly, perturbation of the fastigial nucleus affected ALM activity that abolished

selectivity for the direction of tongue movement along the coding dimension. In contrast, dentate nucleus perturbation changed ALM activity along dimensions orthogonal to the coding dimension, resulting in little effect on behavioural choice. A separate study by Chabrol et al. examined mice navigating a corridor while anticipating a reward and found that the dentate nucleus can drive ALM preparatory activity [14]. These differential engagements of cerebellar nuclei in different behaviors may arise from differential interactions along activity dimensions. The fastigial nucleus may influence the direction of certain types of movement [15,84] whereas the dentate nucleus signals the urgency/timing of upcoming actions [14,50,85]. It remains to be determined whether multiple parallel cortico-cerebellar loops influence activity along specific task-relevant dimensions during motor planning.

Learning transitions between neocortical activity states

The neocortex exhibits sequential activity representing sensory stimuli, behavioural choice or specific movements [86-89], essentially a series of activity states, which emerge as a result of learning [88,89]. Can the cerebellum influence transitions between activity states by learning to drive one pattern of neocortical activity from the previous? These transitions can be established through supervised learning in the cerebellum [59-61], whose mechanisms have been well established for eye blink conditioning [65,90-92] (Fig 4A). During eyeblink conditioning, Purkinje cells learn to associate the inputs from the pontine nucleus (signaling the conditioned stimulus, e.g. tone) with teaching signals from the inferior olive (signaling the unconditioned stimulus, e.g. air puff to eyelid). Once learned, Purkinje cells can produce appropriately timed activity that is triggered by a conditioned stimulus to anticipate a future air puff and drive the predictive eyelid closure [65] (Fig 4A).

We propose that the same supervised learning mechanism allows the cerebellum to learn transitions between relevant neocortical activity states (Fig 4B,D). If one neocortical activity pattern is consistently followed by the next concomitant with a teaching signal, the cerebellum could learn to increase the likelihood of transitions between these states. A possible teaching signal may be any mismatch between the prediction of the future state and the actual neocortical activity pattern [93] (Fig 4C), that may be represented in the inferior olive. Once the new transition is learned, the cerebellum could anticipate and steer the neocortical state transitions (Fig 4B, D). Copies of neocortical activity sent to the cerebellum and resultant cerebellar feedback may steer transitions of neocortical activity to the next predicted state. For example, cerebellar learning mechanism may form new associations between a cortical representation of sensory stimulus with a subsequent movement [94], effectively facilitating sensorimotor transformations. Furthermore, the same mechanism may associate representations of individual movement plans to form a future motor sequence [95], or compensate for unexpected sensory perturbations by learning appropriate transitions that convert output-null neocortical activity states (e.g. related to unexpected

sensory perturbations) into output-potent ones (e.g. activity states representing specific actions) [39,40].

Similar cerebellar plasticity mechanisms that set up transitions between activity states may also support learning of *timing* of these transitions. It is well known that certain frontal and motor neocortical neurons exhibit activity that ramps to a fixed threshold before movement onset [53,96-100]. The speed of ramping predicts movement onset time [51,53,55,96,97], and the slope of ramping is flexibly adjusted depending on the timing of the task [31,101,102]. The ramping activity appears to originate from outside of motor cortex [30,31,51,52,103]. Similar ramps occur in the cerebellar cortical regions that reflect motor planning [14,104]. This ramping signal is consistent with a timing signal that anticipates an upcoming reward or rewarding action [8,11,12,14]. Thus, during goal-directed movement, the cerebellar cortex may compute a ramp in the same way it computes timing during eye blink conditioning [92,105], thereby appropriately adjusting the speed of transitions in neocortical activity states.

Interestingly, recent studies examining motor learning found that the motor cortex activity occupies similar dimensions in activity space before and after the learning but the same activity patterns are quickly re-associated with different motor outputs [106,107]. We suggest that a relatively limited repertoire of neocortical activity states serves as a substrate upon which the cerebellum carries out fast supervised learning to generate appropriate activity transitions, guided by specific teaching signals [94,108]. Recent imaging and electrophysiology recordings in the cerebellum revealed a multitude of teaching signals in climbing fibers that are related to behavioral errors [67,70,94], unexpected reward [11], and anticipatory signals that predict rewarding movement [11,12]. The cerebellum thus has access to sensory, motor, and internal signals, and in theory could guide association of relevant activity states and form transitions between them.

Funneling of trajectories toward activity states is described by attractor dynamics [27,31,109]. Cerebellar feedback connections may help establish specific attractors in motor cortex during motor planning, in addition to the thalamocortical and corticocortical connections. Additional work is needed to incorporate the learned dynamics in the cortico-cerebellar loop into the attractor network.

Closing thoughts

Building on a rich body of literature, we have proposed a conceptual framework for understanding the role of the cerebellum and motor cortex in predictive motor control and learning. In this framework, the cerebellum learns transitions between neocortical activity

states, taking one pattern of activity to drive the next. What signals instruct the cerebellar learning of transitions between neocortical activity states? One possibility is that the teaching signals may be triggered by a mismatch between predictions of the internal model and current neocortical activity pattern (e.g. sensory input) [11,93,94].

To test this theory, it will be important to make use of closed-loop virtual reality and augmented reality behavioural assays within which require the animals to rapidly adjust their motor plans, while monitoring activity in the cerebellum and motor cortex. By introducing controlled sensory events that violate current internal model (e.g. unexpected sensory feedback) [39], one could test for the presence of error-induced activity in the cerebellum, and whether error signals facilitate new transitions in neocortical activity spaces that allow for subsequent behavioural adjustments.

The neocortex may exhibit a relatively fixed set of activity states upon which the cerebellum can learn new activity transitions by rapidly forming associations, guided by the teaching signal. The functional organization in the cerebellum may be related to reciprocal connectivity with neocortical regions, and with combinations of sensory and motor areas [45], potentially allowing the multiplexing of associable neocortical signals. The Purkinje cells in specific cerebellar regions may detect correlated patterns of neocortical activity distributed across multiple areas to steer transitions in neocortical activity sequences required for movement. Elucidating the functional organization of cortical-cerebellar loops and identification of relevant cerebellar regions involved in different tasks is therefore a major open question.

Finally, the cortico-cerebellar loop is part of a larger multi-regional circuit. Motor cortex also forms long-range loops with the basal ganglia and the superior colliculus. These loops also converge in the thalamus [110] and similarly play a role in action selection [111] and motor timing [51]. Resolving the relative contributions of distinct long-range loops during goal-directed behavior will require direct comparisons within the same behavioral task.
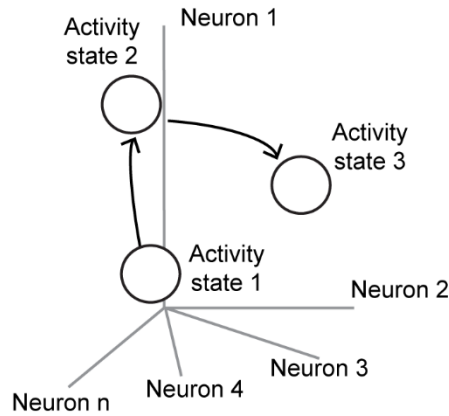
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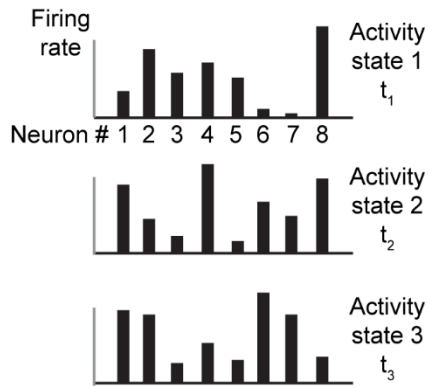
Figure 1 Neocortical activity states and cortico-cerebellar loop. **A.** Patterns of neocortical activity are specific states in activity space. Trajectories in activity space are transitions be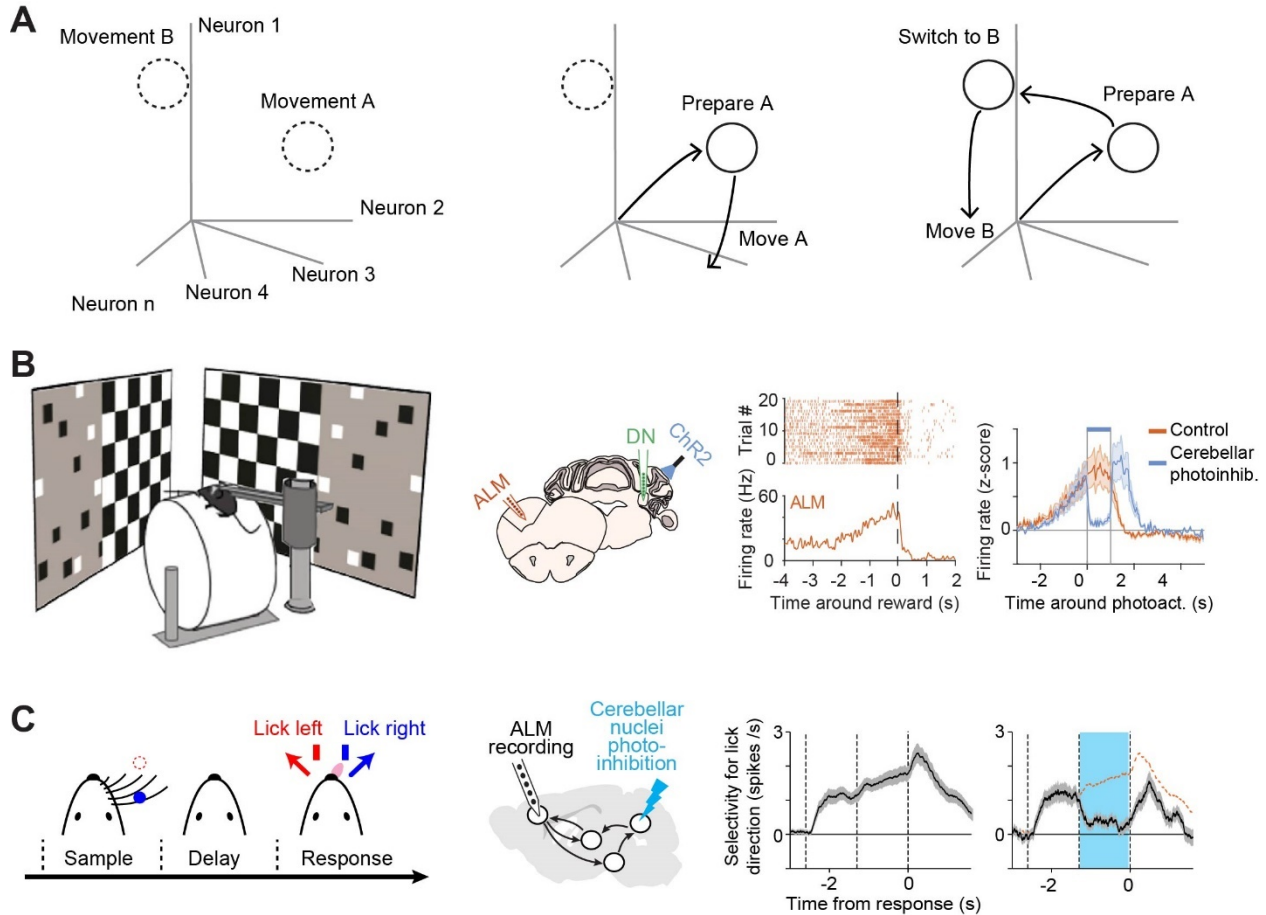tween activity states. **B.** Cortico-cerebellar loop. **C.** Proposed function of the cortico-cerebellar loop. The cerebellum steers transitions between neocortical activity states by using the current state to enable the next, guided by teaching signals.

Figure 2 Preparatory activity mediated by the cortico-cerebellar loop. **A.** Discrete states in activity space correspond to specific movements. Preparatory activity trajectories converge to specific states during motor planning. Once the state is reached, the corresponding movement can be readily triggered. When the trajectory transitions to a different state, a different movement will result. **B.** *Left*, mouse navigating a virtual reality and anticipating reward at a particular location in the corridor indicated by visual landmarks. *Middle*, silicon probe recordings in ALM and the cerebellar nucleus while photoinhibiting the deep cerebellar nucleus. *Right*, preparatory activity in ALM neurons anticipates the stop which is abolished by silencing the cerebellar output [14]. **C.** Mouse performing a delayed response task. ALM preparatory activity anticipates directional licking which is abolished by silencing the cerebellar output [15].
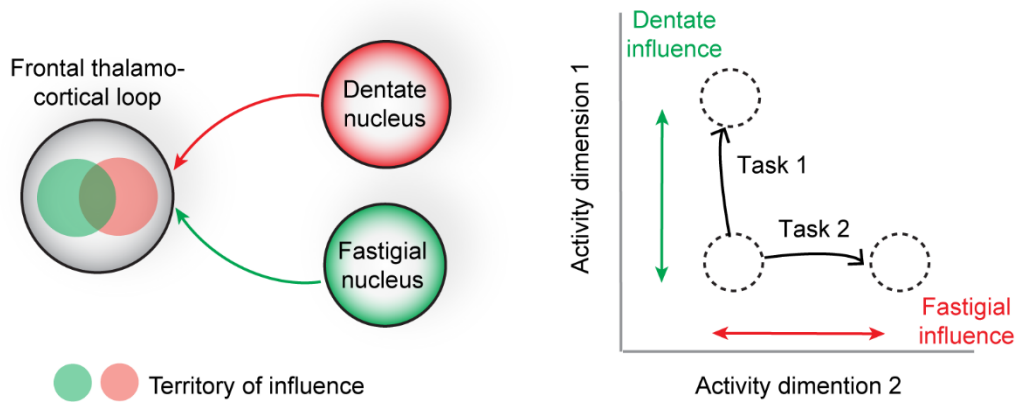
Figure 3 Dimension-specific cortico-cerebellar interactions. *Left*, distinct cerebellar nuclei influence activity in different but overlapping parts of the frontal thalamo-cortical loop. *Right*, distinct cerebellar nuclei influence the motor cortex activity along specific dimensions in activity space. Distinct cerebellar nuclei are differentially engaged by different tasks.
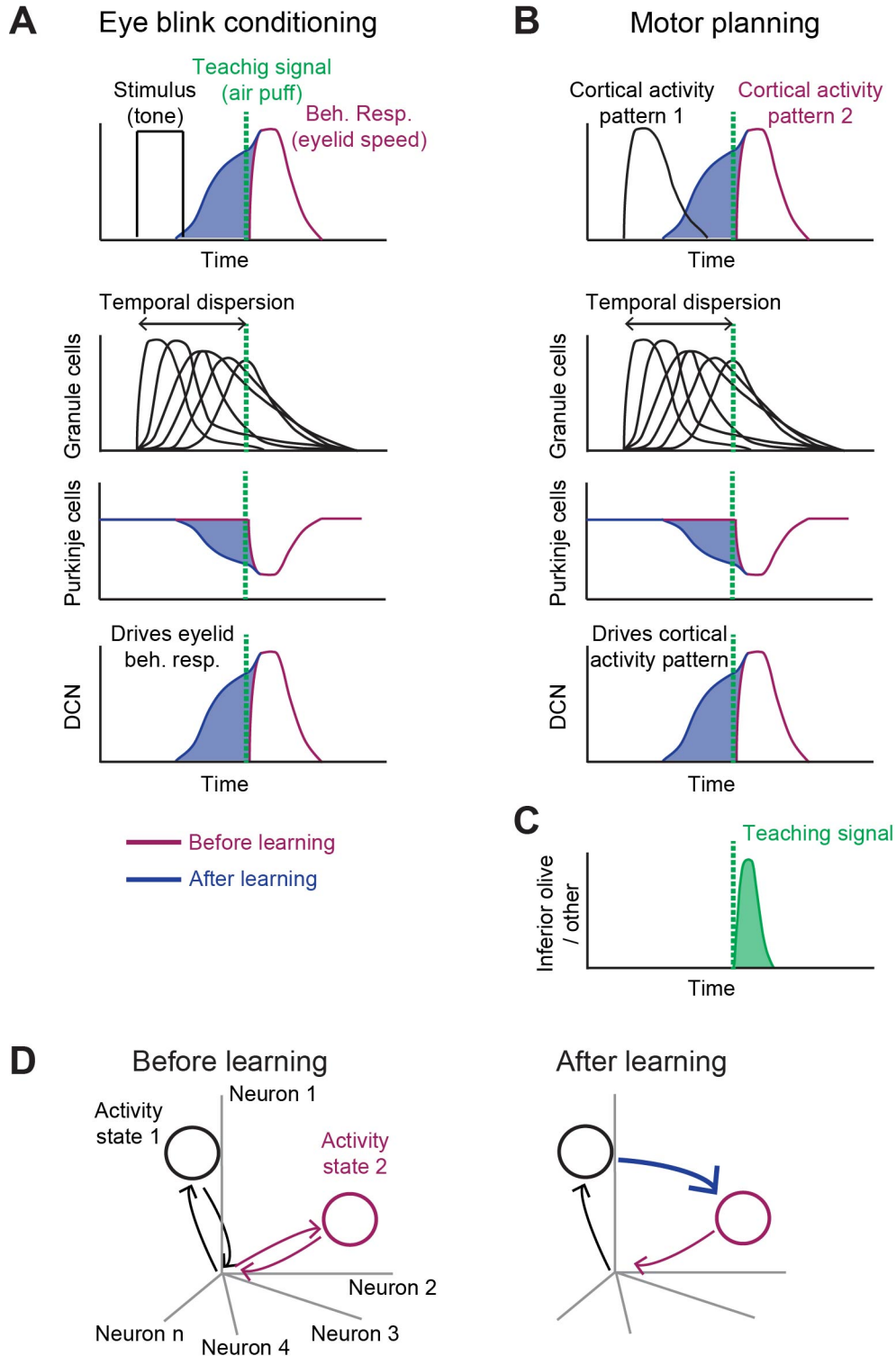
Figure 4 *Hypothesis*: the cerebellum learns to steer transitions between neocortical activity states. **A.** *Top*, during eye blink trace conditioning, a tone (black line) is followed by an aversive air puff (green dashed line), which triggers eyelid closure (purple line). If the tone consistently precedes the air puff, the cerebellum learns to produce anticipatory output

(blue) that is triggered by the tone to drive predictive eyelid closure. *Bottom*, supervised learning mechanism within the cerebellum. The pontine input signaling the tone triggers diverse and temporally dispersed activity in the granule cells [65,66]. The Purkinje cells learn to reweigh the granule cell input via cerebellar LTD, guided by the teaching signal from the inferior olive (green), to produce timed suppression of Purkinje cells in anticipation of the air puff (blue). Once learned, the tone-triggered decrease in Purkinje cell responses disinhibits the deep cerebellar nucleus (DCN) neurons to drive eyelid closure before the air puff. **B.** Hypothetically, the same supervised learning mechanism in the cerebellum can learn to anticipate transitions between neocortical activity states. If one pattern of neocortical activity is consistently followed by another in conjunction with a teaching signal, the cerebellum may learn to generate predictive responses that drive the second neocortical activity pattern. **C**. Putative teaching signal that instructs association between neocortical activity patterns. The teaching signal may reflect an unpredicted occurrence of a neocortical activity pattern. A mismatch between the predicted neocortical activity pattern and the actual activity pattern may be represented in the inferior olive. **D.** Neocortical activity patterns correspond to specific states in activity space. The predictive responses learned by the cerebellum form new transitions between activity states.

Key recent papers:

**Chabrol et al, 2019 (REF 14)

In mice navigating a virtual visual corridor and anticipating a reward, preparatory activity in motor cortex and dentate cerebellar nucleus predict the upcoming reward timing. Preparatory activity in motor cortex requires cerebellar input.

**Wagner et al, 2017 (REF 8)

Cerebellar granule cells signal reward and reward omission. A subset of granule cells exhibit activity that anticipates predictable reward, consistent with expectation of reward.

**Wagner et al, 2019 (REF 13)

Motor cortex and cerebellar granule cells exhibit correlated preparatory activity predicting the direction of upcoming forelimb movement. Correlated activity emerges over learning. Silencing the pontine nucleus reduced cerebellar preparatory activity.

**Gao et al, 2018 (REF 15)

Mouse ALM and cerebellar nuclei exhibit preparatory activity predicting the direction of upcoming licking movement. Silencing ALM abolishes cerebellar preparatory activity. The fastigial cerebellar nucleus drives ALM preparatory activity through the thalamus.

**Proville et al, 2014 (REF 45)

Inputs from the mouse vibrissa somatosensory cortex and vibrissa motor cortex converge in the crus 1 region of the cerebellum, and crus 1 output affects activity in the thalamus and vibrissa motor cortex. The cortico-cerebellar loop contributes to whisker sensorimotor behavior.

**Kunimatsu et al, 2018 (REF 51)

The striatum and dentate cerebellar nucleus exhibit ramping activity before self-timed saccades in nonhuman primates. The slope of ramping activity in the striatum predicts the timing of action, whereas the dentate nucleus exhibits ramping before movement onset.

**Heffley et al, 2018 (REF 12)

In mice performing a visuomotor task, imaging of cerebellar climbing fibers shows the largest response after a movement that leads to a reward. The signal is consistent with predictions of rewarding actions and inconsistent with motor error signals.

**Kostadinov et al, 2019 (REF 11)

Imaging of cerebellar climbing fibers during visuomotor behavior in mice shows a multitude of responses related to sensory, motor, reward, and predictions distributed across cerebellar lobules. The largest response is observed after a predicable rewarding action.

**Heindorf et al, 2018 (REF 39)

In mice navigating a virtual visual corridor, the motor cortex is required for corrective turns in response to unexpected visual perturbations but not for spontaneous turns. Layer 5 neuron activities signal the corrective turns.

**Stavisky et al, 2017 (REF 40)

In nonhuman primates controlling a computer cursor using premotor cortex activity, visuomotor perturbations induce activity that is initially limited to the output-null dimension and later aligns with the output-potent dimension to produce corrections.

**Sendhilnathan et al, 2020 (REF 94)

In nonhuman primates learning to associate visual stimuli with motor responses, Purkinje cells signal the outcome of decisions from the previous trial. The signal diminishes after the new association is learned, consistent with a reinforcement learning signal.

**Khilkevich et al, 2018 (REF 95)

In eye blink conditioning, the cerebellum can learn to use the response from one eyeblink as input to trigger another eyeblink. The result suggests the cerebellum can learn a motor sequence by using feedbacks from one movement to drive the next.

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