Cerebellar degeneration selectively disrupts continuous mental operations in visual cognition

Samuel D. McDougle[1,2,3], Jonathan Tsay[2], Jordan A. Taylor[4,5], & Richard B. Ivry[2,3]

[1]Department of Psychology, Yale University

[2]Department of Psychology, University of California, Berkeley

[3]Helen Wills Neuroscience Institute, University of California, Berkeley

[4]Department of Psychology, Princeton University

[5]Princeton Neuroscience Institute, Princeton University

Correspondence: samuel.mcdougle@yale.edu

ABSTRACT

Various lines of evidence implicate the cerebellum as one node in a network of neural regions engaged in controlled cognitive processes. Characterizing the functional role of the cerebellum within this network, and in cognition more broadly, has proven elusive. Motivated by models of how the cerebellum helps coordinate movement, we propose that the cerebellum contributes to cognitive tasks that involve the transformation of mental representations along a continuous dimension. To test this hypothesis, we compared tasks that entail the continuous transformation of a single visual representation or discrete computations over a set of visual representations. We predicted that individuals with cerebellar degeneration (CD) would be selectively impaired on the former. Consistent with this prediction, two independent CD groups were impaired on a mental rotation task, with the estimated rate of rotation slower than that observed in matched controls. In contrast, the rate required to perform an iterative search through a series of representations in visual (Experiment 1) or visuospatial (Experiment 2) working memory was comparable in the CD and control groups. This dissociation highlights a potential computational constraint on the role of the cerebellum in cognition, setting the stage for future work examining cerebellar contributions to a wider range of behaviors.

INTRODUCTION

It is well established that the functional domain of the cerebellum extends beyond sensorimotor control (Leiner et al., 1986; Schmahmann et al., 2019). Anatomical studies have revealed broad patterns of connectivity between the cerebellum and most of the cerebral cortex in humans and non-human primates, including prominent prefrontal-cerebellar loops with prefrontal cortex (Buckner et al., 2011; Middleton & Strick, 2001; Strick et al., 2009). Work in rodent models has linked cerebellar activity to a variety of surprising non-motor functions, such as reward processing, decision-making, and social interaction (Badura et al., 2018; Carta et al., 2019; Deverett et al., 2018). Human functional neuroimaging studies have revealed consistent cerebellar activation patterns unrelated to overt movement (Buckner, 2013; King et al., 2019; Moberget et al., 2014) and neuropsychological studies have identified a large set of non-motor tasks on which individuals with cerebellar pathology are impaired (Schmahmann et al., 2019).

The most common neuropsychological sequelae in individuals with cerebellar degeneration (CD) are impairments in cognitive control (Alexander et al., 2012), including visuospatial cognition (Malm et al., 1998), working memory (Cooper et al., 2012; Ravizza et al., 2006), and abstract reasoning (Schmahmann & Sherman, 1998). Echoing the loss of motor coordination (movement dysmetria) observed in these patients, the phrase "dysmetria of thought" has been used to summarize seemingly heterogeneous cognitive symptoms associated with CD (Schmahmann, 1991). This phrase reflects the idea that core mental functions such as perception and memory are spared in cerebellar pathology, but the ability to manipulate representations in a coordinated manner is compromised.

At a more computational level, a number of hypotheses have been put forward based on the idea that cerebellar contributions to motor control may generalize to the cognitive domain (Diedrichsen et al., 2019; Ito, 2008). In motor control, computational accounts of cerebellar function have emphasized the importance of this structure in anticipating future states. For example, in coordinating movement, the cerebellum is essential for anticipating the complex forces generated during rapid movements (Therrien & Bastian, 2015). Computationally, the cerebellum is hypothesized to generate predictions of the sensory consequences of a movement, allowing the system to compare this prediction with the actual sensory feedback, ensuring that the sensorimotor system remains precisely calibrated. As such, the computational emphasis is on how the cerebellum can extrapolate the current sensory state to anticipate future sensory states. It may be that putative "dysmetric" cognition in individuals with CD is a consequence of a disrupted ability to continuously anticipate future states, both of the body and of non-motor mental representations.

Here we attempted to test this idea in the domain of visual cognition, exploiting the fact that the manipulation of visual mental representations can be described on a spectrum between continuous and discrete operations (Miller, 1988). Given the continuous manner in which the cerebellum is assumed to anticipate future states to ensure coordinated movement, we reasoned that the integrity of the cerebellum

would be essential for visual cognitive tasks that emphasize a continuous – but not discrete – transformation of mental representations. To test our proposal, we focused on mental rotation as our continuous task, the process by which an internal visual representation is manipulated to facilitate object recognition and visually guided action (Shepard & Metzler, 1971). An extensive body of research provides compelling evidence that mental rotation entails the continuous, putatively movement-like, transformation of a mental representation (Kosslyn, 1981). We hypothesized that individuals with CD would be impaired on mental rotation, with that impairment manifest as a disrupted (slowed) rate of mental rotation.

To test the specificity of our hypothesis, we compared performance on the mental rotation task with two tasks that require participants to perform a more discrete matching operation between stimuli held in mind and a probe stimulus (Georgopoulos & Pellizzer, 1995; Sternberg, 1966). In these tasks we assume the key computation is not continuous, instead entailing the iterative retrieval of a discrete set of representations. Similar to the mental rotation task, this iterative search task also allows us to estimate a rate of mental processing. Here, we predicted that the CD group would not show a disruption in the rate at which they performed discrete operations.

RESULTS

Two groups of adult participants diagnosed with spinocerebellar ataxia due to cerebellar degeneration (CD), and two groups of neurologically healthy controls participated in the experiments. Twelve participants in each group were tested in Experiment 1, and 14 in each group were tested in Experiment 2, with no overlap of individuals between experiments. Each experiment consisted of two tasks. One task was a modified version of a classic mental rotation task (Shepard & Metzler, 1971), with our primary focus on the rate of mental rotation, taken as a measure of the fluidity with which the participants manipulated an internal representation. As control tasks, participants performed variants of two memory search tasks, with a visual working memory search task employed in Experiment 1 (Sternberg, 1966), and a visuo-spatial working memory task in Experiment 2 (Georgopoulos & Pellizzer, 1995; see below for details). The control tasks were selected with three criteria in mind: First, we selected tasks that also tested some aspect of visual cognition. Second, the tasks involved a manipulation that would yield an increase in reaction time as a function of the independent variable. As such, the dependent variable could be expressed in terms of the rate of the underlying operation, echoing our dependent variable for mental rotation. Third, in contrast to mental rotation, the putative mental operation in these tasks should involve an iterative computation that is performed on a series of discrete mental representations, rather than the continuous transformation of a single representation.

Experiment 1

In the mental rotation task, participants were instructed to judge if a visual letter stimulus was normal ("R") or mirror-reflected ("Я"; Figure 1). The stimulus was either presented in its standard upright orientation (0˚), or at one of 10 rotations drawn from the set of [-135˚, -105˚, -75˚, -45˚, -15˚, 15˚, 45˚, 75˚, 105˚, 135˚]. In the second task of Experiment 1 (Figure 1), participants were tested on a memory scanning task. On each trial, the participant viewed either a single, or a sequence of abstract, visual fractal stimuli (sequence length/load = 2-5 stimuli), and, after a brief maintenance period, were asked to judge whether a probe stimulus was a member of the previous sequence (match) or not (non-match). This task is thought to require participants to scan through (serially or in parallel) a set of distinct representations held in working memory.

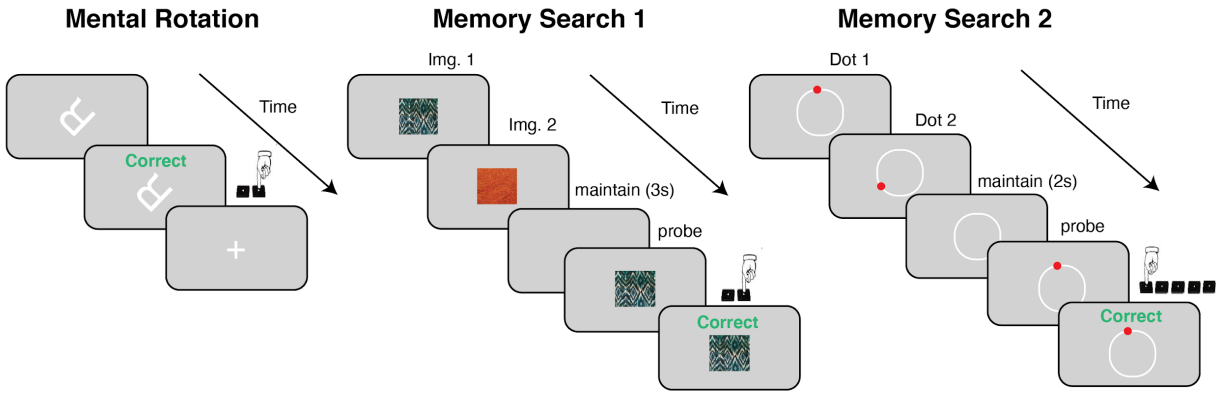

Figure 1: *Design*. In the mental rotation experiment, participants judged if a letter stimulus was normal (e.g., "R", right key press) or mirror-reflected (e.g., "Я", left key press). On most trials, the stimulus was rotated relative to the upright orientation (an example 135˚ trial is shown). The same mental rotation task was used in both Experiments 1 and 2. In the first working memory search task (Experiment 1), a sequence of stimuli (2-5 images) was initially presented (1 s per image). After a maintenance period (3 s), a probe stimulus was presented, and the participant judged whether it was a member of the sequence (right key) or not (left key). Sequences varied in length from one to four items. In the second working memory search task (Experiment 2), a sequence of targets (2-5 items) was presented at random locations on a ring (1 s per target). After a maintenance period (2 s), a probe target was presented, and the participant indicated the ordinal position of the target within the sequence (1-5 on the keyboard). Responses in all tasks were followed by feedback (1 s), and a 1 s inter-trial-interval (ITI).

RT effects

Both mental rotation and working memory search are known to produce a near-linear relationship between RT and the experimentally titrated independent variable, rotation magnitude or set size (i.e., load). Replicating these classic results, regression slopes on the RT data (correct trials only) for both the mental rotation and search conditions were positive (all p_{perm}'s < 0.005) for the control and CD groups (Figure 2). Thus, as expected, absolute rotation magnitude and working memory load induced reliable parametric increases in RT in both groups.

RT intercepts in the mental rotation task were significantly higher in the CD group relative to controls ($p_{perm} = 0.002$), presumably due, at least in part, to motor execution deficits in individuals with ataxia. Our primary interest is the pace of mental rotation, calculated from a regression of RT onto rotation magnitude (see Methods). Consistent with the hypothesis that individuals with cerebellar damage would be impaired in mental rotation relative to controls, an ANCOVA revealed a main effect of group on mental rotation slope, with the CD group showing a higher slope, or slower pace of mental rotation, compared to the control group ($F_{(1, 19)} = 5.67$, $p = 0.03$, Figure 2). We take this increase in slope to be indicative of a disrupted mental rotation process, independent of any motor impairment (which would be expected to produce an additive effect). The results of a two-sample permutation test on the slope values echoed the ANCOVA result, revealing a significant difference in mental rotation slopes between groups ($p_{perm} = 0.009$).

At an individual level, 7 of the 12 CD participants had a slower mental rotation pace than the slowest of the control participants. Slopes were not related to age ($F_{(1, 19)} = 0.05$, $p = 0.83$), nor MoCA scores ($F_{(1, 19)} = 4.14$, $p = 0.06$).

Opposite the result observed at the group level, two individuals in the CD group showed the fastest mental rotation paces (lowest slopes) overall. We note that these two participants also had the highest error rates on the task, responding correctly on fewer than 75% of trials (Figure 3a). Although speculative, it may be that these individuals had such difficulty performing mental rotation that they instead opted to make intuited responses based on the presented orientation of the stimuli. Unsurprisingly, if these two participants are excluded from the slope analysis, the resulting group difference is also significant ($p_{\text{perm}} = 0.004$).

Similar to the mental rotation task, RT intercepts in the search task (i.e., average RTs when there was no load, sequence length = 1) were significantly higher in the CD group relative to controls ($p_{\text{perm}} < 0.001$). However, in contrast to the mental rotation task, an ANCOVA did not reveal a significant main effect of group on the RT slope ($F_{(1, 19)} = 2.80$, $p = 0.11$, Figure 2). Here, the slope results revealed that the average memory search pace for the CD group was actually faster than the average pace for the controls. Thus, although individuals with CD were globally slower to respond than the controls on this task, the non-significant difference in slopes suggests that they were unimpaired in the particular processing requirements for searching through discrete items in visual working memory. Slopes were not affected by age ($F_{(1, 19)} = 0.66$, $p = 0.43$), MoCA scores ($F_{(1, 19)} = 0.01$, $p = 0.92$), nor baseline RTs ($F_{(1, 19)} = 0.42$, $p = 0.52$). The results of a two-sample permutation test also failed to reveal a difference in slopes between groups ($p_{\text{perm}} = 0.16$).

The dissociation between the mental rotation and search tasks suggests that the slower pace of rotation observed in the CD group does not reflect a global impairment in cognitive processing, the motor demands of the tasks, or differential sensitivity to fatigue (Timmann & Daum, 2007) . Rather, the regression analyses point to a selective impairment, one associated with a mental operation requiring the continuous transformation of an internal representation.

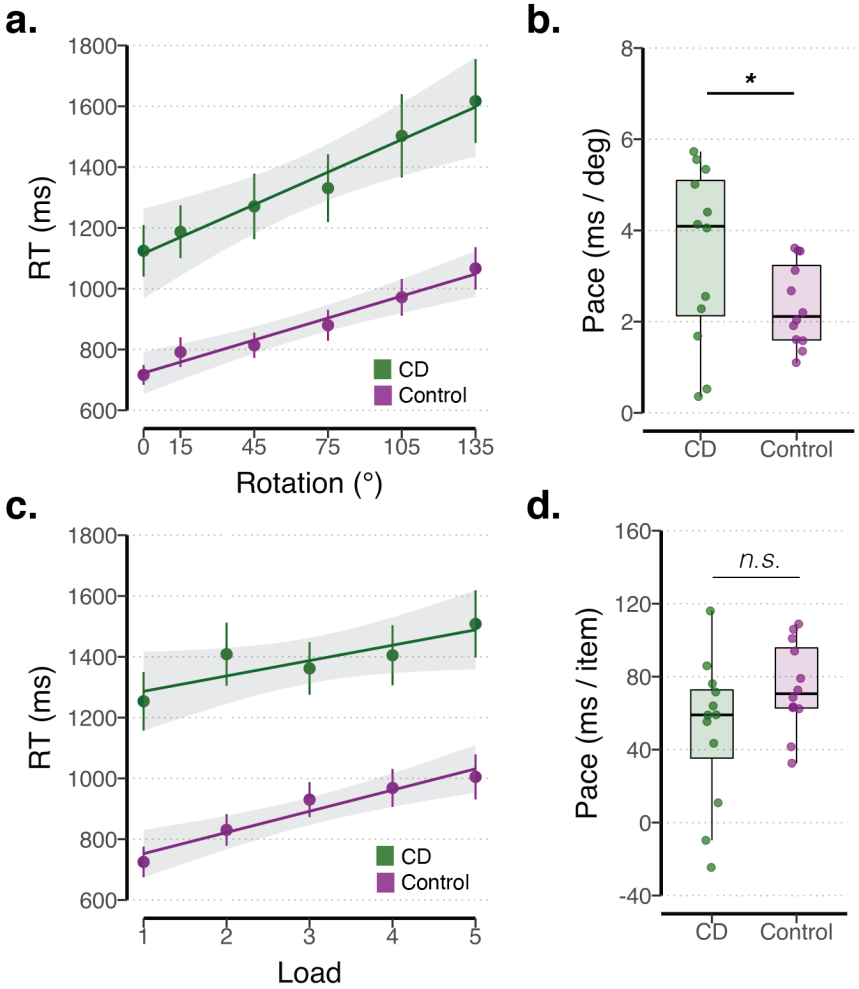

Figure 2: *Cerebellar degeneration is associated with disrupted rate of mental rotation, but not working memory search*. **(a)** Mean RT as a function of stimulus rotation on the mental rotation task for the CD group (green) and the control group (purple). **(b)** Estimated rate of rotation from the regression analysis (slope of RT function). **(c)** Mean RT as a function of memory load on the visual working memory task. **(d)** Estimated search rate from the regression analysis. Mean regression lines are displayed in a and c. Error bars = 1 s.e.m. * $p < 0.05$.

Accuracy effects

Although our hypotheses focused on RT, we also examined accuracy on the two tasks (Figure 3a). Overall performance was relatively higher on the mental rotation task (93.2%, SD = 7.2) than on the memory search task (85.7%, SD = 6.7). The control group performed better than the CD group in both tasks, a difference that was significant for the mental rotation task ($F_{(19)} = 7.51$ $p = 0.01$) and the search task ($F_{(19)} = 24.72$, $p < 0.001$). The latter results replicate previously reported accuracy deficits in individuals with CD on working memory tasks (Molinari et al., 2004; Schmahmann & Sherman, 1998). Accuracy in the mental rotation task was affected by age ($F_{(19)} = 6.72$, $p = 0.02$), baseline RT ($F_{(19)} = 10.12$, $p < 0.001$),

and MoCA scores ($F_{(19)} = 5.72$, $p = 0.03$), but accuracy in the memory search task was affected by age only ($F_{(19)} = 4.78$, $p = 0.04$).

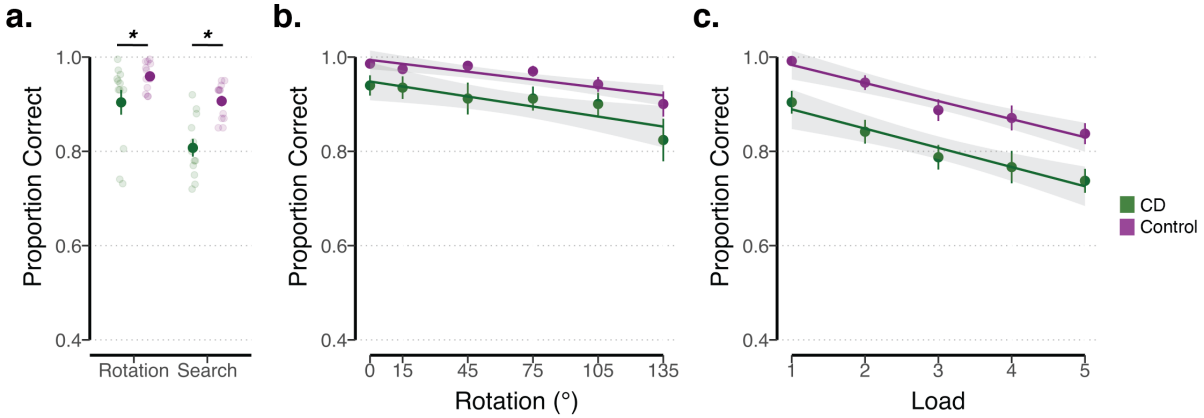

Figure 3: *Accuracy differences between groups are independent of rotation angle and memory load.* **(a)** Overall accuracy rate is lower for CD group compared to controls on both tasks (dark dots=group means; light dots=individual scores). Mean proportion correct as a function of rotation **(b)** and load **(c)** for the rotation and memory search tasks, respectively. Mean regression lines are displayed in b and c. Error bars = 1 s.e.m. * $p < 0.05$.

Given the group accuracy differences on both tasks, it is important to consider if the dissociation observed between the tasks in the slope analyses might arise from a difference in speed-accuracy tradeoffs. To examine this question, we performed another regression analysis, but now used accuracy as the dependent variable (Figure 3b, c). The effect of rotation magnitude and load led to decreases in accuracy in both tasks, but the slope relating the independent variables to accuracy was not significantly different between groups (rotation: $p_{perm} = 0.77$; search: $p_{perm} = 0.50$). Thus, the regression analyses provide no indication that the CD impairment in accuracy became more pronounced, relative to controls, with larger rotations or load, arguing against a speed-accuracy tradeoff account of the RT results.

Experiment 2

As noted above, the main constraint in selecting a control task was that variation in the independent variable produce a parametric increase in RT (similar to mental rotation), but with the RT increase assumed to reflect a discrete mental operation. However, one could argue that an additional difference between the tasks in Experiment 1 is that the mental rotation task is more spatial in nature than the memory search task. We used abstract, fractal-like images in the search task to discourage verbal encoding; nonetheless, the processing requirements for this task would seem to be less demanding on spatial cognition than mental rotation. Thus, the observed dissociation in Experiment 1 might be taken to suggest a selective role for the cerebellum in spatial computations.

To test this alternative hypothesis, we paired the mental rotation task with a new control task that specifically taxed visuospatial working memory (Figure 1). Here, a sequence of targets was presented on a visual ring, and after a delay period, a probe stimulus was displayed. The position of the probe matched the position of one of the previously viewed targets. The participant indicated the ordinal position of the probe within the observed sequence by pressing one of five numbered keys. By varying the length of the sequence (2-5 locations), RT was expected to increase, presumably because of variation in the load imposed on spatial working memory. This task is modeled after Georgopoulos & Pellizzer (1995), although in that study, participants reached to the location of the subsequent ordinal item in the memory set relative to the probe. We opted to require simple ordinality judgments (i.e., button presses) to minimize the motor demands of the task and create a better match for the mental rotation task. Moreover, pilot studies with control participants indicated that reports of the cued item rather than the subsequent item in the list was sufficiently challenging to produce a robust load effect.

If cerebellar degeneration specifically impacts spatial processing rather than continuous computations, we expect to observe an increase in slope in the CD group relative to the control participants on both the mental rotation task and spatial working memory search task. However, if the dissociation described in Experiment 1 is replicated, Experiment 2 would provide further support for the continuous transformation hypothesis.

RT effects

Regression slopes (RT X rotation magnitude/load; correct trials only) were significantly positive for both groups in the mental rotation and working memory search tasks (Figure 4; all p's$_{perm} < 0.001$). Thus, as expected, absolute rotation magnitude and load induced increases in RT in both groups. Similar to Experiment 1, RT intercepts in the mental rotation task were significantly longer in the CD group relative to controls ($p_{perm} = 0.002$).

Critically, we replicated the between-group slope difference on the mental rotation task: An ANCOVA again revealed a main effect of group, with the CD group showing a higher slope compared to the control group ($F_{(1, 23)} = 6.50$, $p = 0.02$, Figure 4a, b); this difference was also seen via a two-sample permutation test ($p_{perm} = 0.03$). Mental rotation slopes were not affected by MoCA scores ($F_{(1, 23)} = 2.05$, $p = 0.17$) nor baseline RTs ($F_{(1, 23)} = 0.86$, $p = 0.36$). The effect of age was significant, ($F_{(1, 23)} = 5.19$, $p = 0.03$), with older participants showing slower rotation paces. An informal between-experiment comparison showed that the mean mental rotation slope values observed in Experiment 2 (controls: 2.20, CD: 3.19) were similar to those observed in Experiment 1 (controls: 2.36, CD: 3.47).

In contrast to the mental rotation task, there was no group effect on slopes in the spatial memory search task ($F_{(1, 23)} = 0.04$, $p = 0.85$, Figure 4c, d). Thus, the individuals with cerebellar pathology appeared

to be unimpaired in terms of the processing required to search through a discrete set of spatial locations in working memory. This null result was echoed in a two-sample permutation test ($p_{perm} = 0.85$). Slopes were neither affected by age ($F_{(1, 23)} < 0.001$, $p = 0.997$) nor MoCA scores ($F_{(1, 23)} = 0.02$, $p = 0.89$). We did not include a baseline RT factor in the spatial memory search analysis since we did not include a condition in which the memory load was one.

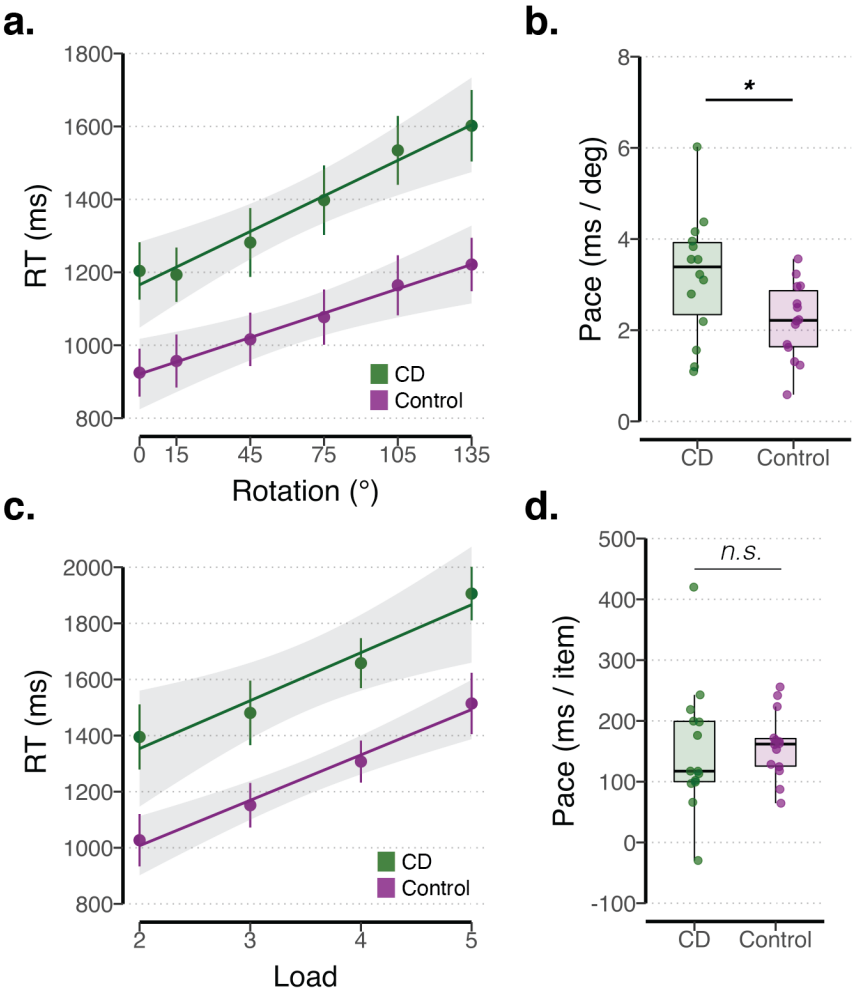

Figure 4: *Impairment in manipulation of spatial information is found for mental rotation, but not search through spatial working memory.* In a replication of experiment 1, **(a-b)**, CD group (green) showed slower mental rotation speeds relative to controls (purple). Mental rotation paces are plotted with the absolute rotation magnitude of the stimulus on the x-axis, and the mean change in RTs for each rotation condition on the y-axis. In the search task **(c-d)**, the two groups showed comparable spatial memory search speeds. The length of the test sequence (load) is plotted on the x-axis, and the mean change in RTs for each load condition on the y-axis. Mean regression lines are displayed on panels a and c. Error bars = 1 s.e.m. * $p < 0.05$.

Accuracy effects

In terms of accuracy (Figure 5a), overall performance was higher on the mental rotation task (94.2%, SD = 4.29) compared to the memory search task (77.8%, SD = 11.26). While the difference may reflect differences in the difficulty of the computations needed for each task, it is also important to note that

the number of response options differs for the two tasks, and thus the chance performance level (two options in mental rotation, chance level is 50%; five in memory search, chance level between 50% - 20% depending on load). Unlike Experiment 1, accuracy scores were not significantly different between the CD and control groups on the mental rotation task ($F_{(1, 23)} = 0.33$, $p = 0.57$). However, the CD group performed significantly worse in the memory search task ($F_{(1, 23)} = 6.42$, $p = 0.02$), consistent with previous findings (Molinari et al., 2004). Effects of age ($F_{(1, 23)} = 0.002$, $p = 0.97$), baseline RT ($F_{(1, 23)} = 0.51$ $p = 0.48$), and MoCA scores ($F_{(1, 23)} = 1.85$, $p = 0.19$) were not significant in the ANCOVA. Accuracy in the memory search task was positively affected by MoCA scores only ($F_{(19)} = 4.78$, $p = 0.03$).

As in Experiment 1, we tested for a speed-accuracy tradeoff account of the slope result (Figure 5b, c): Again, the effect of rotation magnitude and load on task accuracy was consistently negative, as expected, but was not significantly different between groups (rotation; $p_{perm} = 0.74$; search; $p_{perm} = 0.97$).

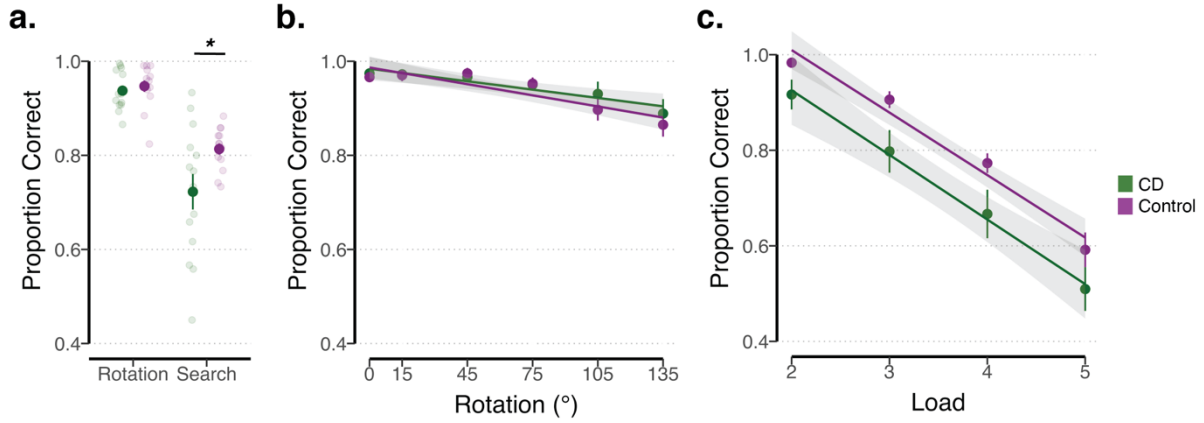

Figure 5: *Accuracy is a function of rotation angle and memory load, with group difference only observed on the search task.* **(a)** Overall accuracy rate is lower for CD group compared to controls on only the search task (dark dots=group means; light dots=individual scores). Effects of independent task variables (rotation magnitude in panel **(b)** and load in panel **(c)** could not explain group differences. Error bars = 1 s.e.m. * $p < 0.05$.

DISCUSSION

The cerebellum, and cerebellar-like structures, are a major neuroanatomical feature of the central nervous system, strikingly conserved across the vertebrate subphylum. A large body of experimental and theoretical work has yielded detailed models of how this structure supports sensorimotor learning and motor control. In contrast, while the involvement of the cerebellum in cognition has been highlighted in many studies since the seminal conjecture of Leiner, Leiner, and Dow (1986), our understanding of how the cerebellum supports cognition at a computational level remains limited. The homogeneous anatomy and physiology of the cerebellum has inspired the idea that the cerebellum applies a universal algorithm (Diedrichsen et al., 2019; Schmahmann et al., 2019), or what has been called a "universal cerebellar transform" (UCT). In contrast, the diverse patterns of task-related activity observed in neuroimaging studies of the human cerebellum might be taken to imply a heterogeneous role for the cerebellum in cognition (Keren-Happuch et al., 2014; King et al., 2019). However, the functional diversity inferred from these studies likely reflects input to the human cerebellum (Lauritzen, 2001), with a UCT being applied to these inputs to support a broad range of behaviors. While recognizing that homogenous structure and physiology need not imply homogenous function, the UCT concept can be useful in generating computational hypotheses.

Here we build on this idea, seeking to identify constraints on the type of cognitive operations that rely on the integrity of the cerebellum. Inspired by the cerebellum's role in motor coordination, we propose one such constraint -- that the cerebellum is specifically leveraged in tasks that require the continuous transformation of a mental representation. Putatively, the distinction between continuous and discrete defines one dimension for describing the transformations between mental states (Miller, 1988). As an initial test of the continuous transformation hypothesis, we focused on the domain of visual cognition. We tested two independent groups of individuals with cerebellar degeneration (CD) and matched controls, on two distinct types of visual cognition tasks, one continuous (mental rotation) and one discrete (working memory search). Reaction time slopes, taken as a proxy for the core transformative mental operation required in these tasks, were elevated in the CD group for mental rotation but not for visual (Experiment 1) nor spatial (Experiment 2) memory search. These findings point to a causal role for the cerebellum in visual cognition and suggest that this role may be specific to the optimization of continuous mental transformations.

The continuous transformation hypothesis is related to previous theoretical conjectures that take, as their starting point, the idea that cerebellar computations for motor control may generalize to more cognitive domains (Ito, 2008). One such conjecture stems from the idea that the cerebellum generates internal models for predictive control (Wolpert et al., 1998), and in particular is part of a network that uses inverse models to compute the motor commands required to bring about a desired sensory state. In motor control, such a model could help compute the transformation needed to guide a limb in a continuous manner

from position A to position B. Mental rotation could be described as a similar kind of continuous state transition problem; e.g., how do I rotate this object from orientation A to orientation B? To date, an extension of the internal model idea as an explanatory hypothesis to account for cerebellar cognitive function has emphasized the idea of manipulation and prediction in a general sense. Thus, any manipulation of information in working memory would fall within the functional domain of the cerebellum. In contrast, our current proposal focuses on a specific way in which the cerebellum may support the manipulation of mental representations, namely those that entail a continuous transformation. The corollary of this is that the cerebellum is not essential when the manipulation entails more discrete transformations.

Along these lines, the current results provide an explanation for some puzzling results in the sensorimotor adaptation literature. It has long been recognized that cerebellar damage produces marked impairments on adaptation tasks, such as visuomotor rotation (Schlerf et al., 2013; Taylor et al., 2010; Tseng et al., 2007). However, recent work has made clear that learning in such tasks may entail multiple processes, prominent among these being the use of a flexible aiming strategy; for example, a clockwise perturbation can be compensated for by aiming in the counterclockwise direction from the target (McDougle et al., 2016; Taylor et al., 2014). Recent studies have shown that individuals with CD are not only impaired in implicit adaptation, but also on the cognitive strategic component of visuomotor learning (Butcher et al., 2017; Wong et al., 2019). Interestingly, their impairment in using an aiming strategy was primarily manifest as "under-aiming", choosing a strategy that failed to fully compensate for the perturbation. The continuous transformation hypothesis suggests that this deficit is not a generic problem in strategy use, but rather arises because aiming requires a form of mental rotation. That is, an initial movement plan is directed at the target and then parametrically rotated to produce the desired strategy (Georgopoulos & Pellizzer, 1995; McDougle & Taylor, 2019). According to this perspective, the under-aiming observed in the CD group is another manifestation of an impairment in mental rotation. A slower rotation rate with a (roughly) unchanged decision bound would result in the observed under-aiming.

A limitation of our study is that we observed two group differences not accounted for by the continuous transformation hypothesis. First, the CD group was consistently slower to respond in all tasks and conditions. We assume some of the increase in RT is related to the motor deficits associated with CD. However, baseline RT differences were around 322 ms across the two mental rotation tasks and 470 ms across the two working memory tasks, values somewhat larger than those observed in studies involving similar participant groups (e.g., Breska & Ivry, 2018). Second, although not dependent on load, the CD group had worse accuracy than the control group on the mental rotation task in Experiment 1 and on both of the memory search tasks, (Figures 3a, 5a). Taken together, these results suggest that, in addition to the specific impairment on mental rotation, the CD participants may also have more generic, non-motor impairments on the tasks used here.

Moreover, while some neuropsychological studies have reported cognitive deficits in CD that are consistent with the continuous transformation hypothesis (e.g., Molinari et al., 2004), other studies have revealed impairments that appear to be inconsistent or orthogonal to the hypothesis. For example, in motor sequence learning, patients with cerebellar pathology display deficits in learning arbitrary stimulus-response contingencies but perform normally when those contingencies are directly cued (Spencer & Ivry, 2009). This dissociation does not seem to have a clear link to a distinction between continuous and discrete transformations. Future experiments, employing behavioral tasks designed to test precise claims about underlying cognitive processes, will be important to arbitrate between different hypotheses of cerebellar cognitive function, and more generally, the utility of the UCT framework.

Going forward, the continuous representational transformation hypothesis can be extended to explore the role of the cerebellum across a broad range of cognitive domains. By postulating a core constraint on cerebellum computation, this hypothesis can be used to generate falsifiable predictions in other cognitive domains. For instance, humans are thought to traverse a "mental number line" when performing simple arithmetic computations, manipulating a given numeric representation in a continuous manner (e.g., addition of small numbers by successive increments; Dehaene et al., 1993). The continuous representational transformation hypothesis would predict that individuals with CD would be impaired on such mathematical operations, but not when the mathematical tasks can be solved in a more discrete manner (e.g., retrieval of rote mathematical knowledge). In a similar manner, future studies involving a broad range of cognitive tasks could provide a testbed to evaluate if a hallmark of cerebellar processing centers on the continuous transformation of bodily and mental states.

METHODS

Participants

Adult participants diagnosed with spinocerebellar ataxia due to cerebellar degeneration (N = 26) and neurologically healthy controls (N = 26) participated in the study in exchange for monetary compensation ($20 per hour). Each participant completed one experiment (12 per group in Experiment 1; 14 per group in Experiment 2). The protocol was approved by the institutional review boards at Princeton University and the University of California, Berkeley.

Participants with CD displayed clinical signs associated with cerebellar atrophy, assessed at the time of testing with the Scale for Assessment and Rating of Ataxia (SARA; Schmitz-Hubsch et al., 2006; see Table 1). In most cases, the diagnosis was confirmed from a combination of family history, genetic profiling, and MRI. Twelve of the 26 individuals with ataxia had an identified CD subtype; for the other individuals, genetic testing was inconclusive or absent. Nine of the CD participants tested in Experiment 2 were related, accounting for the large proportion of individuals with SCA-6 in this experiment.

Control participants were roughly matched to the clinical sample by age (Experiment 1: CD = 49.8 years, range = 37-70, Control = 50.2, range = 35-68; Experiment 2: CD = 57.2 years, range = 32-71, Control = 50.7, range = 33-73 years) and gender (Experiment 1: 5 of 12 females in both groups; Experiment 2: 11 and 10 females in the CD and control groups, respectively). Age-matching was less successful in Experiment 2 as our priority was on education matching (CD = 15.8 years, range = 12 - 22; Control = 16.4, range = 13 – 20; education data not collected for Experiment 1). We also recorded participants' handedness, as measured by the Edinburgh Handedness Inventory (Oldfield, 1971).

All participants were screened for general cognitive deficits using the Montreal Cognitive Assessment. Inclusion required that the participant achieve a score above 20 points. The score on this test, as well as age, were included as covariates in the primary analyses (see below).

General Procedure and Apparatus

Each experiment involved testing participants on two experimental tasks. One task, mental rotation, was identical in both experiments. The other task was one of two variants of a visual working memory search task. The stimuli were displayed, and responses recorded, on a laptop computer (MacBook Pro, Apple) running the psychophysics toolbox package (Brainard, 1997) for MATLAB (MathWorks). Participants were seated at a comfortable distance from the screen (viewing distance ~40 cm) and responded with their right hand which was positioned over the computer keyboard. Participants were visually monitored by the experimenter to make sure no overt strategic movements (e.g., head tilting) were made during the tasks. The order of tasks was counterbalanced across participants, and both were completed in a

single session. Each task took approximately 40 minutes to complete, and a ten-minute break was provided between the two tasks.

Exp.	ID	Age	Sex	Handedness	MoCA	SARA	Etiology	Years of Education
Exp. 1	p1	38	F	Right	28	7.5	SCA-1	
	p2	39	M	Right	27	9.5	SCA-1	
	p3	38	F	Right	28	6	SAOA	
	p4	52	M	Right	26	15.5	SAOA	
	p5	40	F	Right	29	5	SAOA	
	p6	70	F	Right	29	19.5	SAOA	
	p7	62	M	Right	28	17.5	SCA-1	
	p8	57	F	Right	29	8.5	SCA-5	
	p9	37	M	Right	26	21.5	SAOA	
	p10	61	M	Right	29	12.5	SCA-15	
	p11	51	M	Left	28	7.5	SAOA	
	p12	52	M	Right	27	10.5	SAOA	
Exp. 2	pp1	62	F	Right	28	14.5	SCA-3	16
	pp2	60	F	Right	22	7.0	SCA-6	12
	pp3	67	F	Right	24	25.0	SCA-6	12
	pp4	32	M	Right	21	5	SAOA	16
	pp5	57	F	Right	27	10.5	SAOA	18
	pp6	66	F	Right	24	11.5	SAOA	17
	pp7	57	F	Right	22	15.5	SAOA	12
	pp8	71	F	Right	23	7.5	SCA-6	16
	pp9	50	M	Right	26	16	SAOA	20
	pp10	65	F	Right	26	13	SCA-6	16
	pp11	38	F	Right	27	13.5	SAOA	16
	pp12	65	F	Right	27	12.5	SCA-6	22
	pp13	50	F	Right	26	2	SAOA	12
	pp14	61	M	Right	26	4.5	SCA-6	16

Table 1: *Demographic and clinical assessment of the CD participants.* MoCA scores are out of a total of 30 points. SARA scores are out of a total of 40 points (most severe ataxia). SCA = spinocerebellar ataxia; SAOA = spontaneous adult onset ataxia.

Mental Rotation

Following the basic design of Shephard and Metzler (1971), participants were instructed to judge if a visual stimulus was normal ("R") or mirror-reflected ("Я"; Figure 1). Eight capitalized sans-serif (Helvetica font) letter stimuli were used, consisting of normal and reflected versions of the letters F, G, J, and R (Young et al., 1980) . Letter stimuli were white and presented on a black background. To minimize the need for any eye movements while maintaining stimulus legibility, the stimuli were modestly sized (~4 cm^2), of high contrast, and were presented centrally on each trial.

Participants were instructed to press the right arrow key with their right ring finger when the stimulus, if viewed in an upright orientation, was in standard form, and the left arrow key with their right index finger when, if viewed in an upright orientation, the stimulus was mirror reflected. The stimulus was presented in its standard upright orientation (0˚, baseline condition), or rotated, using one of 10 angles drawn from the set of [-135˚, -105˚, -75˚, -45˚, -15˚, 15˚, 45˚, 75˚, 105˚, 135˚]. The stimulus remained visible until the response, or for 5 s. After each response, feedback was shown above the letter stimulus for 1 s. On correct trials, the word "correct" was displayed in green font. On incorrect trials, the word "incorrect" was displayed in red font. Participants were instructed to respond quickly, but without sacrificing accuracy. If no response was made by 5 s, the message "too slow" was displayed in red font. Following a 1 s feedback interval, the display was replaced by a white fixation cross (0.9 cm^2) for a 2 s inter-trial interval.

Participants performed 18 total trials at each rotation size and sign, intermixed with 36 no-rotation baseline trials, for a total of 216 trials. Stimuli were presented in a pseudo-random order, with an equal number of presentations of each stimulus (normal versus reflected) at each rotation sign and magnitude. Prior to the start of the experimental block, the participants performed five practice trials to ensure that they understood the task instructions and were comfortably positioned to respond on the keyboard.

Working Memory Search

Two variants of visual working memory search tasks were used as control tasks (Figure 1). For Experiment 1, we used a variant of the "memory scanning" task introduced by Sternberg (1966). For Experiment 2, we adopted a spatial memory working memory task employed by Georgopoulos and Pellizzer (1995).

In the non-spatial variant, participants viewed a brief sequence of visual stimuli on each trial, and, after a maintenance period, were instructed to judge whether a probe stimulus was a member of the previous sequence (match) or not (non-match). The stimuli consisted of 30 colorful fractal-like patterns, generated using the randomization function of ArtMatic Pro (www.artmatic.com). The images were cropped to be square-shaped and were matched in size to the mental rotation stimuli (4 cm^2). To start each trial, a sequence of fractal images was shown, with each image displayed at the center of the screen for 1 s (with no inter-stimulus interval). The number of stimuli in a sequence ranged from one to five items, thus varying the memory load across trials. After the sequence terminated, the screen was blanked for a maintenance period of 3 s. A probe stimulus was then presented. Participants were instructed to press the right arrow key with their right ring figure in the event of a match, and the left arrow with their right index finger in the event of a non-match. The probe remained visible until the response or until 5 s had elapsed. Feedback ("correct",

"incorrect", "too slow") was displayed above the probe stimulus for 1 s after the response was made. The display was then replaced by a white fixation cross for a 2 s inter-trial interval.

On 50% of the trials, the probe matched one of the items in the sequence, and on the other 50% of the trials, the probe did not match any of the items. Twenty trials at each load were presented (10 match, 10 non-match) in a pseudo-random order for a total of 100 trials. Participants completed five practice trials at the start of the experiment.

In the spatial memory search task, participants viewed a sequence of circular red targets (diameter 1.2 cm), displayed on a white ring (radius 7 cm). A target could be presented at any location from 0˚ - 345˚ (at multiples of 15˚), with the constraint that no target location be repeated in a given sequence. Each target was presented alone for 800 ms, with no time gap between successive targets. The number of targets in the sequence ranged from 2 to 5 items. After the end of the sequence, the white ring remained on the screen for a maintenance period of 2 s, after which a probe target was shown. The probe target always appeared in one of the positions previously shown in the sequence. Participants were instructed to press the number on the keyboard corresponding to the ordinal position of the probe within the sequence (i.e., "1" key = first item, "2" key = second item, etc.). As in the non-spatial search task (Experiment 1), the probe remained visible until the response, and feedback was presented for 1 s following the response. During the 2 s inter-trial interval, the white ring remained visible.

Each load level (i.e., sequence length) was presented 30 times in a randomized order, for a total of 120 trials. Within each load condition, probe positions were sampled uniformly between the first and the second-to-last position; for example, if the load was 5, the probe location could match the location of the first, second, third, or fourth target in the sequence. Except for the load = 2 condition, we chose not to include trials probing the terminal position, given the asymmetrically large RT benefit for this position observed in pilot testing. The task started with five practice trials to ensure that participants understood the instructions.

Analysis

Trials associated with extreme outlier RTs (> ± 3.5 sd from the participant's mean) were removed prior to the RT analysis (percentage of removed trials: Mental Rotation: 1.0% ± 0.4% and 1.2 ± 0.5% for Experiments 1 and 2, respectively; Non-Spatial Search: 1.1 ± 0.6%; Spatial Search: 1.2 ± 0.8%).

All three tasks have been shown to produce a parametric function relating the main independent variable, absolute rotation magnitude in mental rotation or load in working memory search, to RT. Given this, we computed the slope of the RT functions using each participant's raw RTs in a general linear regression model assuming gamma distributed residuals. This regression analysis was performed on correct trials only. We opted to use a model based on the gamma distribution given that this provides a better

488 approximate for RT distributions compared to the normal distribution (Lo & Andrews, 2015; McGill &
489 Gibbon, 1965; Ratcliff, 1979). Parametric assumptions were tested using the Shapiro-Wilk test for
490 normality and Levene's test for homogeneity of variance. When parametric assumptions were met (which
491 was the case for accuracy data), statistical tests were performed on the mean values; when these assumptions
492 were violated (which was the case for RT slope distributions in all groups/experiments), non-parametric
493 permutation tests were employed.

494 Several analyses on participants' baseline RT data (i.e., trials with load = 1 in memory search and
495 rotation = 0˚ in mental rotation) revealed that the groups were not matched on baseline RTs; that is, the CD
496 group was, overall, globally slower in responding across all tasks and conditions. Thus, we opted to use
497 ANCOVAs including each individual's median-centered baseline RT, and also including MoCA score and
498 age as covariates in the critical analysis of the RT slope data. We chose this approach given that the groups
499 were not well-matched on age in Experiment 2, and because, *a priori*, we expected performance on the
500 cognitive tasks might vary with clinical and/or demographic variables (e.g., MoCA and age). As a
501 complementary analysis, we also used two-tailed permutation tests to compare slopes, with alpha set at 0.05
502 (non-parametric tests were used due to failure to meet parametric assumptions). All statistical tests were
503 conducted with R (GNU).

REFERENCES

Alexander, M. P., Gillingham, S., Schweizer, T., & Stuss, D. T. (2012). Cognitive impairments due to focal cerebellar injuries in adults. *Cortex*, *48*(8), 980–990. https://doi.org/10.1016/j.cortex.2011.03.012

Badura, A., Verpeut, J. L., Metzger, J. W., Pereira, T. D., Pisano, T. J., Deverett, B., Bakshinskaya, D. E., & Wang, S. S.-H. (2018). Normal cognitive and social development require posterior cerebellar activity. *ELife*, *7*, e36401. https://doi.org/10.7554/eLife.36401

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*, 433–436.

Breska, A., & Ivry, R. B. (2018). Double dissociation of single-interval and rhythmic temporal prediction in cerebellar degeneration and Parkinson's disease. *Proceedings of the National Academy of Sciences*, *115*(48), 12283–12288. https://doi.org/10.1073/pnas.1810596115

Buckner, R. L. (2013). The Cerebellum and Cognitive Function: 25 Years of Insight from Anatomy and Neuroimaging. *Neuron*, *80*(3), 807–815. https://doi.org/10.1016/j.neuron.2013.10.044

Buckner, R. L., Krienen, F. M., Castellanos, A., Diaz, J. C., & Yeo, B. T. T. (2011). The organization of the human cerebellum estimated by intrinsic functional connectivity. *Journal of Neurophysiology*, *106*(5), 2322–2345. https://doi.org/10.1152/jn.00339.2011

Butcher, P. A., Ivry, R. B., Kuo, S.-H., Rydz, D., Krakauer, J. W., & Taylor, J. A. (2017). The cerebellum does more than sensory prediction error-based learning in sensorimotor adaptation tasks. *Journal of Neurophysiology*, *118*(3), 1622–1636.

Carta, I., Chen, C. H., Schott, A. L., Dorizan, S., & Khodakhah, K. (2019). Cerebellar modulation of the reward circuitry and social behavior. *Science*, *363*(6424), eaav0581. https://doi.org/10.1126/science.aav0581

Cooper, F. E., Grube, M., Von Kriegstein, K., Kumar, S., English, P., Kelly, T. P., Chinnery, P. F., & Griffiths, T. D. (2012). Distinct critical cerebellar subregions for components of verbal working memory. *Neuropsychologia*, *50*(1), 189–197. https://doi.org/10.1016/j.neuropsychologia.2011.11.017

Dehaene, S., Bossini, S., & Giraux, P. (1993). The mental representation of parity and number magnitude. *Journal of Experimental Psychology: General*, *122*(3), 371–396. https://doi.org/10.1037/0096-3445.122.3.371

Deverett, B., Koay, S. A., Oostland, M., & Wang, S. S.-H. (2018). Cerebellar involvement in an evidence-accumulation decision-making task. *ELife*, *7*, e36781. https://doi.org/10.7554/eLife.36781

Diedrichsen, J., King, M., Hernandez-Castillo, C., Sereno, M., & Ivry, R. B. (2019). Universal Transform or Multiple Functionality? Understanding the Contribution of the Human Cerebellum across Task Domains. *Neuron*, *102*(5), 918–928. https://doi.org/10.1016/j.neuron.2019.04.021

Georgopoulos, A. P., & Pellizzer, G. (1995). The mental and the neural: Psychological and neural studies of mental rotation and memory scanning. *Neuropsychologia*, *33*(11), 1531–1547.

Ito, M. (2008). Control of mental activities by internal models in the cerebellum. *Nature Reviews Neuroscience*, *9*(4), 304–313. https://doi.org/10.1038/nrn2332

Keren-Happuch, E., Chen, S.-H. A., Ho, M.-H. R., & Desmond, J. E. (2014). A meta-analysis of cerebellar contributions to higher cognition from PET and fMRI studies: A Meta-Analysis of Cerebellar Contributions. *Human Brain Mapping*, *35*(2), 593–615. https://doi.org/10.1002/hbm.22194

King, M., Hernandez-Castillo, C. R., Poldrack, R. A., Ivry, R. B., & Diedrichsen, J. (2019). Functional boundaries in the human cerebellum revealed by a multi-domain task battery. *Nature Neuroscience*, *22*(8), 1371–1378. https://doi.org/10.1038/s41593-019-0436-x

Kosslyn, S. (1981). The medium and the message in mental imagery: A theory. *Psychological Review*, *88*(1), 46–66.

Lauritzen, M. (2001). Relationship of Spikes, Synaptic Activity, and Local Changes of Cerebral Blood Flow. *Journal of Cerebral Blood Flow & Metabolism*, *21*(12), 1367–1383. https://doi.org/10.1097/00004647-200112000-00001

Leiner, H. C., Leiner, A. L., & Dow, R. S. (1986). Does the cerebellum contribute to mental skills? *Behavioral Neuroscience*, *100*(4), 443–454. https://doi.org/10.1037/0735-7044.100.4.443

Lo, S., & Andrews, S. (2015). To transform or not to transform: Using generalized linear mixed models to analyse reaction time data. *Frontiers in Psychology*, *6*. https://doi.org/10.3389/fpsyg.2015.01171

Malm, J., Kristensen, B., Karlsson, T., Carlberg, B., Fagerlund, M., & Olsson, T. (1998). Cognitive impairment in young adults with ipfratentorial infarcts. *Neurology*, *51*(2), 433–440.

McDougle, S. D., Ivry, R. B., & Taylor, J. A. (2016). Taking Aim at the Cognitive Side of Learning in Sensorimotor Adaptation Tasks. *Trends in Cognitive Sciences*, *20*(7), 535–544. https://doi.org/10.1016/j.tics.2016.05.002

McDougle, S. D., & Taylor, J. A. (2019). Dissociable cognitive strategies for sensorimotor learning. *Nature Communications*, *10*(1). https://doi.org/10.1038/s41467-018-07941-0

McGill, W. J., & Gibbon, J. (1965). The general-gamma distribution and reaction times. *Journal of Mathematical Psychology*, *2*(1), 1–18. https://doi.org/10.1016/0022-2496(65)90014-3

Middleton, F. A., & Strick, P. L. (2001). Cerebellar Projections to the Prefrontal Cortex of the Primate. *The Journal of Neuroscience*, *21*(2), 700–712. https://doi.org/10.1523/JNEUROSCI.21-02-00700.2001

Miller, J. (1988). Discrete and continuous models of human information processing: Theoretical distinctions and empirical results. *Acta Psychologica*, *67*(3), 191–257. https://doi.org/10.1016/0001-6918(88)90013-3

Moberget, T., Gullesen, E. H., Andersson, S., Ivry, R. B., & Endestad, T. (2014). Generalized Role for the Cerebellum in Encoding Internal Models: Evidence from Semantic Processing. *Journal of Neuroscience*, *34*(8), 2871–2878. https://doi.org/10.1523/JNEUROSCI.2264-13.2014

Molinari, M., Petrosini, L., Misciagna, S., & Leggio, M. (2004). Visuospatial abilities in cerebellar disorders. *Journal of Neurology, Neurosurgery, and Psychiatry*, *75*(2), 235–240.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*(1), 97–113.

Ratcliff, R. (1979). Group reaction time distributions and an analysis of distribution statistics. *Psychological Bulletin*, *86*(3), 446–461. https://doi.org/10.1037/0033-2909.86.3.446

Ravizza, S. M., McCormick, C. A., Schlerf, J. E., Justus, T., Ivry, R. B., & Fiez, J. A. (2006). Cerebellar damage produces selective deficits in verbal working memory. *Brain*, *129*(2), 306–320. https://doi.org/10.1093/brain/awh685

Schlerf, J. E., Xu, J., Klemfuss, N. M., Griffiths, T. L., & Ivry, R. B. (2013). Individuals with cerebellar degeneration show similar adaptation deficits with large and small visuomotor errors. *Journal of Neurophysiology*, *109*(4), 1164–1173. https://doi.org/10.1152/jn.00654.2011

Schmahmann, J. D. (1991). An Emerging Concept: The Cerebellar Contribution to Higher Function. *Archives of Neurology*, *48*(11), 1178. https://doi.org/10.1001/archneur.1991.00530230086029

Schmahmann, J. D., Guell, X., Stoodley, C. J., & Halko, M. A. (2019). The Theory and Neuroscience of Cerebellar Cognition. *Annual Review of Neuroscience*, *42*(1), null. https://doi.org/10.1146/annurev-neuro-070918-050258

Schmahmann, J. D., & Sherman, J. C. (1998). The cerebellar cognitive affective syndrome. *Brain : A Journal of Neurology*, *121*(), 561–579. https://doi.org/10.1093/brain/121.4.561

Schmitz-Hubsch, T., du Montcel, S. T., Baliko, L., Berciano, J., Boesch, S., Depondt, C., Giunti, P., Globas, C., Infante, J., Kang, J.-S., Kremer, B., Mariotti, C., Melegh, B., Pandolfo, M., Rakowicz, M., Ribai, P., Rola, R., Schols, L., Szymanski, S., … Klockgether, T. (2006). Scale for the assessment and rating of ataxia: Development of a new clinical scale. *Neurology*, *66*(11), 1717–1720. https://doi.org/10.1212/01.wnl.0000219042.60538.92

Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science*, *171*(3972), 701–703.

Spencer, R. M., & Ivry, R. B. (2009). Sequence learning is preserved in individuals with cerebellar degeneration when the movements are directly cued. *Journal of Cognitive Neuroscience*, *21*(7), 1302–1310.

Sternberg, S. (1966). High-speed scanning in human memory. *Science*, *153*(3736), 652–654.

Strick, P. L., Dum, R. P., & Fiez, J. A. (2009). Cerebellum and Nonmotor Function. *Annual Review of Neuroscience*, *32*(1), 413–434. https://doi.org/10.1146/annurev.neuro.31.060407.125606

Taylor, J. A., Klemfuss, N. M., & Ivry, R. B. (2010). An explicit strategy prevails when the cerebellum fails to compute movement errors. *The Cerebellum*, *9*(4), 580–586.

Taylor, J. A., Krakauer, J. W., & Ivry, R. B. (2014). Explicit and implicit contributions to learning in a sensorimotor adaptation task. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *34*(8), 3023–3032. https://doi.org/10.1523/JNEUROSCI.3619-13.2014

Therrien, A. S., & Bastian, A. J. (2015). Cerebellar damage impairs internal predictions for sensory and motor function. *Current Opinion in Neurobiology*, *33*, 127–133. https://doi.org/10.1016/j.conb.2015.03.013

Timmann, D., & Daum, I. (2007). Cerebellar contributions to cognitive functions: A progress report after two decades of research. *The Cerebellum*, *6*(3), 159–162. https://doi.org/10.1080/14734220701496448

Tseng, Y.-W., Diedrichsen, J., Krakauer, J. W., Shadmehr, R., & Bastian, A. J. (2007). Sensory prediction errors drive cerebellum-dependent adaptation of reaching. *Journal of Neurophysiology*, *98*(1), 54–62. https://doi.org/10.1152/jn.00266.2007

Wolpert, D. M., Miall, R. C., & Kawato, M. (1998). Internal models in the cerebellum. *Trends in Cognitive Sciences*, *2*(9), 338–347. https://doi.org/10.1016/S1364-6613(98)01221-2

Wong, A. L., Marvel, C. L., Taylor, J. A., & Krakauer, J. W. (2019). Can patients with cerebellar disease switch learning mechanisms to reduce their adaptation deficits? *Brain*, *142*, 12.

Young, J. M., Palef, S. R., & Logan, G. D. (1980). The Role of Mental Rotation in Letter Processing by Children and Adults. *Canadian Journal of Experimental Psychology*, *34*(3), 265–269.