Cerebellar degeneration selectively disrupts continuous mental operations

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ABSTRACT

Inspired by computational models of how the cerebellum supports the coordination of movement, we propose a novel hypothesis to specify constraints on how this subcortical structure contributes to higher-level cognition. Specifically, we propose that the cerebellum helps facilitate dynamic continuous transformations of mental representations (CoRT). To test this hypothesis, we compared the performance of individuals with cerebellar degeneration (CD) on tasks that entail continuous movement-like mental operations with tasks that entail more discrete mental operations. In the first pair of experiments, individuals with CD were impaired on a mental rotation task, showing a slower rate of mental rotation compared to control participants. In contrast, the rate at which they scanned discrete representations in visual working memory was similar to that observed in the control group. In the second pair of experiments, we turned to mathematical cognition as a test of the generality of the CoRT hypothesis. Individuals with CD were selectively impaired in adding single-digit numbers, a task hypothesized to entail a mental operation involving continuous transformations along a mental number line. In contrast, their rate of performing arithmetic operations thought to involve retrieval from a look-up table was unimpaired. These results, obtained in disparate task domains, suggest a general role for the cerebellum in coordinating dynamic transformations in mental space, paralleling key features of computational theories concerning the cerebellum's role in coordinated movement.

INTRODUCTION

Multiple lines of investigation have 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 reciprocal connections between the cerebellum and 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 mostly spared in cerebellar pathology, but that the ability to manipulate mental 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 the motor domain, computational accounts of cerebellar function have emphasized the importance of this structure in anticipating future states. For example, in coordinating movement, the cerebellum is hypothesized to generate predictions of the sensory consequences of a movement. This prediction is compared with observed sensory feedback, with the difference used as an error signal to ensure that the sensorimotor system remains precisely calibrated (Wolpert et al., 1998). As such, the emphasis in such models is on how the cerebellum can extrapolate from the current sensory state to anticipate future sensory

states. Extending this idea to cognition has motivated hypotheses about a general cerebellar role in prediction, and in particular, how the cerebellum may be required for mental simulation to anticipate future cognitive states given the current input (Ito, 2008). According to this view, the "dysmetric cognition" associated with CD could be seen as a consequence of a disrupted ability to anticipate future physical and mental states.

Prediction is, of course, a general feature of brain function. As such, a core challenge is to specify the boundary conditions, or constraints, associated with how a specific brain region or network contributes to prediction. In terms of motor control, one important constraint arises from the fact that movement entails the continuous transformation of the body; a movement goal may be couched in terms of a desired end state, prompting the motor system to transform the body's initial state to the desired end state in an efficient way. Computational models of the cerebellum have focused on its role in this optimization process, ensuring that this dynamic state transformation is implemented in a smooth and continuous manner. Here we extend this idea to cognition, building on the observation that the manipulation of mental representations can be described on a spectrum between continuous and discrete operations (Miller, 1988). We propose that the cerebellum is essential for mental operations that require continuous representational transformations, what we will refer to for brevity as the "CoRT" hypothesis. A corollary of the CoRT hypothesis is that the role of the cerebellum is minimized for mental operations that operate in a more discrete manner.

Here we test this hypothesis in two disparate non-motor domains: visual cognition and arithmetic. For visual cognition, an extensive body of behavioral and physiological research provides compelling evidence that operations involved in visual imagery and mental rotation entail continuous representational transformations (Kosslyn, 1981). For example, in mental rotation, the manipulation of a visual representation to facilitate object recognition requires movement through intermediate representational states (Shepard & Metzler, 1971; 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. We compared performance on this mental rotation task with performance on two versions of a visual working memory task in which participants compared a probe stimulus to a set of stimuli held in memory (Georgopoulos & Pellizzer, 1995; Sternberg, 1966). Unlike in mental rotation tasks, it is unclear what if any intermediate states people could generate to support this comparison process. We

therefore assume that the rate-limiting computation in these matching tasks is not continuous, but instead reflects an iterative process involving the discrete retrieval and evaluation of a set of representations. We predicted that the CD group would not show a disruption in the rate at which they perform this operation.

For mental arithmetic, we leveraged the concept of the mental number line, an implicit spatial representation thought to support basic mathematical operations such as magnitude comparison and simple addition (Restle, 1970; de Hevia, Izard, Coubart, Spelke, & Streri, 2014; de Hevia, Veggiotti, Streri, & Bonn, 2017). For example, patients with spatial neglect from right hemisphere lesions show systematic biases when mentally bisecting numerical intervals (e.g., stating 16 as midpoint between 12 and 18), similar to the rightward bias they exhibit in bisecting physical lines (Zorzi et al., 2002; see also Longo & Lourenco, 2007; Dehaene, 1999; Hubbard et al., 2005). In terms of simple arithmetic, reaction time increases in a linear manner with the magnitude of the operands (Verguts, & Van Opstal, 2005), and error patterns are suggestive of operational momentum along a number line, inducing a bias to overestimate the solution to addition problems and underestimate the solution to subtraction problems (McCrink, Dehaene, & Dehaene-Lambertz, 2007).

Although more contentious than claims about the analog nature of mental rotation, these findings support the notion that many basic arithmetic operations are performed in a continuous mental space. As such, we predicted that individuals with CD would be impaired on tasks that require such transformations. We used a numeric verification task involving the addition of two single-digit numbers, predicting that the CD group would show, like mental rotation, a steeper magnitude effect than control participants. For our control tasks, we selected two numeric operations that are thought to rely on rote retrieval: Addition problems involving the same number (e.g., 3 + 3) and single-digit multiplication (e.g., 5 * 6). For the former, reaction times are largely independent of the magnitude of the operand (Groen, Parkman, 1972; Campbell, 1995); for the latter, RT increases with magnitude, but here the increase is attributed to a look-up operation that is mediated by problem frequency (Campbell & Xue, 2001; LeFevre et al., 1996). To the extent that these identity addition problems and multiplication problems are memorized, solving them should not require a continuous transformation of a mental representation (e.g., “moving” four units along a number line to verify whether 3 + 4 = 7), but rather a discrete sampling of information from memory. We therefore predicted that performance on these

problems (i.e. identity addition and multiplication) would be similar in the CD and control groups.

RESULTS

Experiment 1a

Using visual cognition tasks, we asked whether individuals diagnosed with spinocerebellar ataxia due to cerebellar degeneration (n = 12) would exhibit a selective impairment on a CoRT-dependent operation, compared to their age- and gender- matched controls (n = 12). For our CoRT task (Fig 1), we employed a classic mental rotation task (Shepard & Metzler, 1971), given the compelling evidence that mental rotation entails the continuous transformation of an internalized stimulus representation. Participants judged if a visual letter stimulus was normal ("R") or mirror-reflected ("Я"), where the stimulus was rotated by a particular degree on each trial: [-135˚, -105˚, -75˚, -45˚, -15˚, 0˚, 15˚, 45˚, 75˚, 105˚, 135˚]. For our non-CoRT-dependent task, we employed a variant of a classic memory search task (Sternberg, 1966) presumed to require an iterative (or parallel) search through a set of discrete visual representations held in working memory. Participants viewed a single or sequence of abstract, visual fractal stimuli (set size 1-5), and, after a brief maintenance period, were asked to judge whether a probe stimulus was a member of the set (match) or not (non-match).

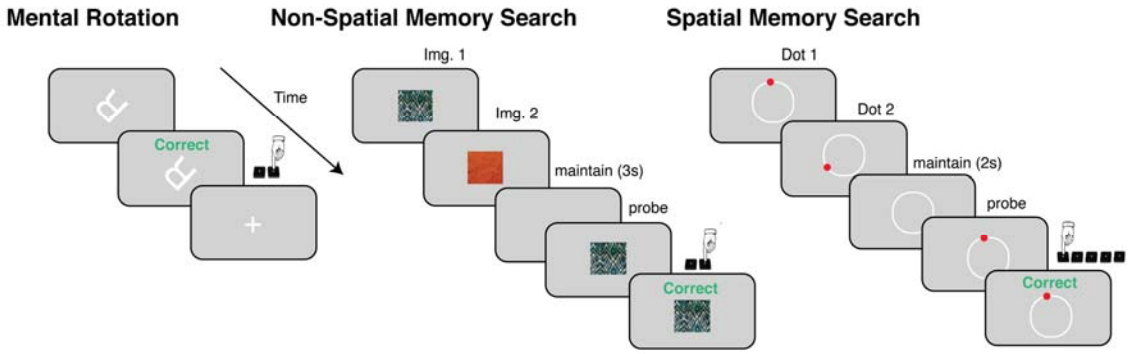

Figure 1: Task progression for Exp 1a and 1b. *Visual Cognition Tasks.* In the mental rotation experiment, participants judged if a letter stimulus was normal (e.g., "R", right key press) or mirror-reflected (e.g., "Я", left key press). On most trials, the stimulus was rotated relative to the upright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

RT effects

We first assessed whether the results with both groups were in accord with the classic finding observed with these two tasks, namely that RTs increase with the experimentally titrated independent variable – rotation magnitude for mental rotation and set size for visual memory search. Replicating these classic results, regression slopes on the RT data from the correct trials from both tasks were significantly positive (all p_{perm}'s < 0.005) for the control and CD groups (Fig 2): Participants took more time to respond for larger rotations and larger set sizes.

We compared behavior between the groups for each task, starting with the mental rotation task. The estimated intercept from the regression analyses of the mental rotation data was significantly higher in the CD group relative to Controls (p_{perm} = 0.002; CD = 1122 $\pm$ 239 ms; Control = 725 $\pm$ 125 ms), presumably due, at least in part, to motor execution deficits in individuals with ataxia. Our main interest is in the slope estimates, which index the rate of mental rotation (i.e., milliseconds per degree of rotation). An ANCOVA revealed a main effect of group, with the CD group showing a greater slope compared to the control group ($F_{(1, 20)}$ = 4.5, p = 0.04). We interpret this increase in slope as indicative of a slower rate of mental rotation independent of any motor impairments, given that the latter would be expected to produce only an intercept effect. On average, the rate of rotation for the Controls was 2.2 ms/deg, whereas the rate for the CD group was 3.2 ms/deg, an increase of approximately 45% relative to the Controls. Using a more conservative non-parametric post-hoc assessment (two-sample permutation test, 1000 permutations), the CD mental rotation slopes remained significantly greater than Controls (p_{perm} = 0.01), corroborating the results from the ANCOVA. While slopes were not related to age ($F_{(1, 20)}$ = 0.8, p = 0.37), there was a significant main effect of baseline RTs scores ($F_{(1, 20)}$ = 9.6, p < 0.001). Slower baseline RTs were associated with larger slopes, an effect that did not differ for the CD and Control groups.

At an individual level, 7 of the 12 CD participants had slower mental rotation rates than the slowest of the control participants. Interestingly, two individuals in the CD group showed the fastest mental rotation rates (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 (Fig 3a). Although speculative, it may be that the difficulty these individuals had in mental rotation led them to use an alternative strategy, making intuited responses based only on the presented

orientation of the stimuli. Unsurprisingly, if these two participants are excluded from the slope analysis, the resulting group difference remains significant ($p_{\text{perm}} = 0.004$).

Turning to the data from the memory search task, we again observed a group difference in the estimated RT intercept, with the mean value higher in the CD group relative to Controls ($p_{\text{perm}} < 0.001$). In contrast to the mental rotation results, the effect of group was not significant on the RT slope estimates ($F_{(1, 20)} = 3.1$, $p = 0.09$). Indeed, the average memory search rate for the CD group was actually faster than the average rate for the Controls (51 ms/item in CD vs 74 ms/item in Controls). The results of a two-sample permutation test also failed to reveal a difference in slopes between groups ($p_{\text{perm}} = 0.16$). The slopes were neither affected by age ($F_{(1, 20)} = 1.5$, $p = 0.24$) nor by baseline RT ($F_{(1, 20)} = 0.9$, $p = 0.3$).

To directly compare RT slopes across the two tasks, which we note each had different independent variables (rotation degrees vs set size), we used a permutation test on the group-level effect sizes (see *Methods*). This comparison revealed a significant interaction between group and task, with the rate difference between groups being much larger for mental rotation compared to visual memory search ($d_{Rotation} - d_{Search} = 1.45$, $p_{perm} < 0.001$). This dissociation suggests that the slower pace of rotation observed in the CD group did not reflect a global impairment in cognitive processing, and also argues against a motoric account of the group differences (Timmann & Daum, 2007). Rather, the analyses point to a selective impairment in the mental rotation task, consistent with the hypothesis that the integrity of the cerebellum is essential for efficiently coordinating the continuous transformation of an internal representation (CoRT).

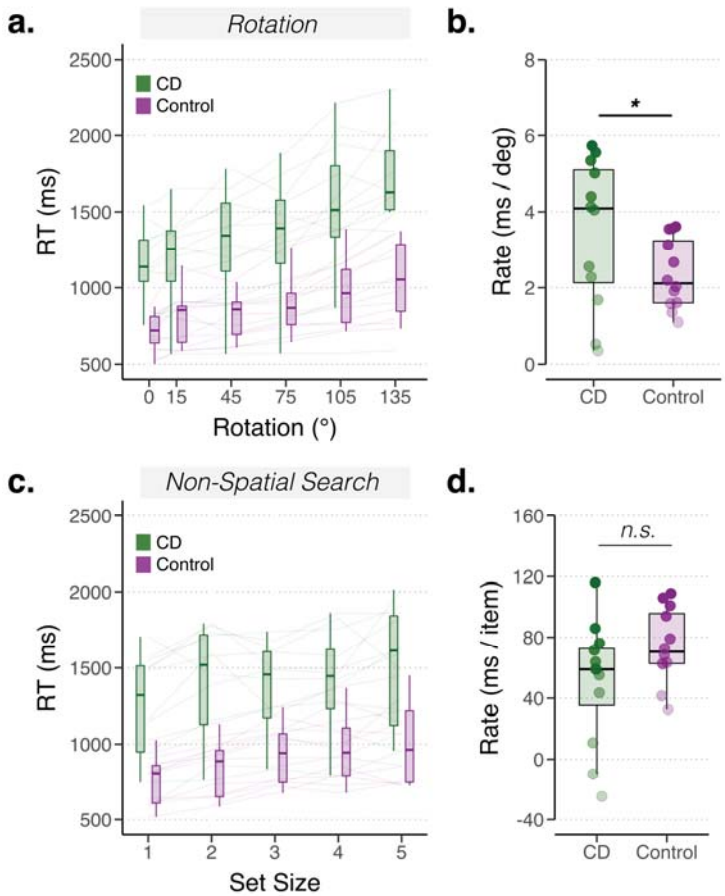

Figure 2: Reaction time analysis for Exp 1a. *Cerebellar degeneration is associated with a slower rate of mental rotation but does not impact the rate of search through visual working memory*. **(a)** Median RT as a function of stimulus orientation in the mental rotation task for the CD group (green) and the control group (purple). **(b)** Estimated rate of rotation from the regression analysis (slope of RT function). **(c)** Median RT as a function of set size in the visual memory search task. **(d)** Estimated search rate from the regression analysis. Thin lines denote individual RT functions in **(a)** and **(c)**. Box and whisker plots delineate the median, 1st/3rd quartile, and max/min. * $p < 0.05$.

Accuracy effects

Although our predictions focused on RT, we also examined accuracy on the two tasks (Fig 3a). Performance was 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 had higher accuracy scores than the CD group in both the mental rotation task ($F_{(1, 20)} = 5.7$, $p = 0.03$) and memory search task ($F_{(1, 20)} = 19.8$, $p < 0.001$). 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 ($F_{(1, 20)} = 1.3$, $p = 0.27$) and

baseline RT ($F_{(1, 20)}$ = 10.3, p = 0.004); however, accuracy in the memory search task was not affected by either variable (age: $F_{(1, 20)}$ = 1.2, p = 0.28; baseline RT: $F_{(1, 20)}$ = 0.04, p = 0.85).

Given the group difference in accuracy on both tasks, it is important to consider whether 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 set of regression analyses but now used accuracy as the dependent variable (Figs 3b, c). The effect of rotation magnitude and set size led to decreases in accuracy in both tasks. However, the slopes were not different between groups (rotation: p_{perm} = 0.77; search: p_{perm} = 0.50; task X group interaction: $d_{Rotation} - d_{Search} = -0.13$, $p_{perm} = 0.59$). Thus, the regression analyses provide no indication that the CD impairment in accuracy became more pronounced, relative to Controls, with larger rotations or increases in set size, arguing against a speed-accuracy tradeoff account of the RT results.

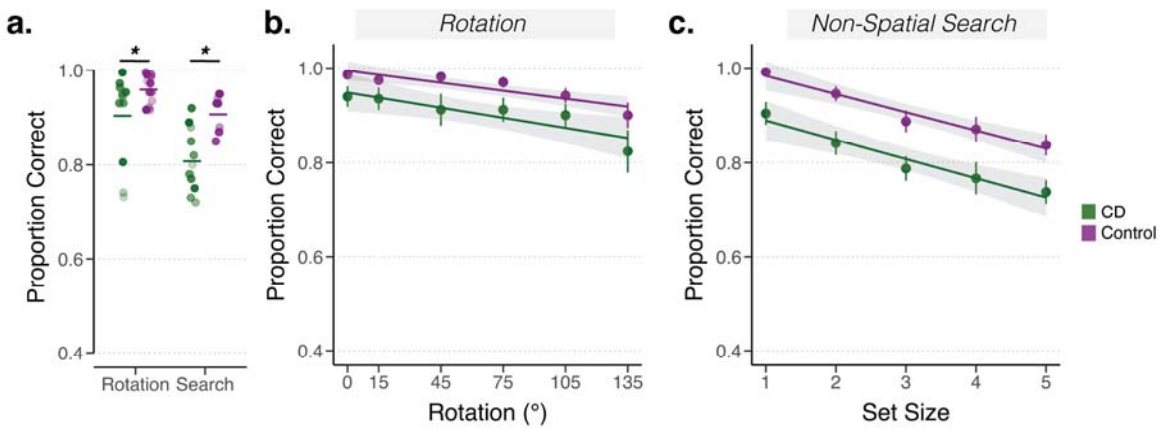

Figure 3: Accuracy analysis for Exp 1a. *Accuracy differences between groups are independent of rotation angle and set size in working memory.* **(a)** Overall accuracy rate is lower for the CD group compared to the Control group on both tasks (dots are shaded according to the within-group ranking of mental rotation and search rates, as seen in Figs 2b and 2d, with the darkest shade denoting the slowest rate and the lightest shade denoting the fastest rate; horizontal line indicates group means). Mean proportion correct as a function of rotation **(b)** and set size **(c)** for the rotation and memory search tasks, respectively. Mean regression lines are displayed in **(b)** and **(c)**. Shaded error bars denote 1 s.e.m. * p < 0.05.

Experiment 1b

As noted above, the main factor in selecting a control task was that variation in the independent variable should produce a parametric increase in RT, with that independent variable assumed to reflect a mental operation performed in an iterative manner on a set of discrete

representations. We recognize, however, that there are many differences between mental rotation and visual memory search, with one notable difference being that the former is spatial in nature. Thus, the observed dissociation could reflect a selective role for the cerebellum in spatial cognition (Leggio et al., 2000), rather than a selective role in facilitating continuous representational transformations.

We conducted a second visual cognition experiment to evaluate this alternative hypothesis, pairing the mental rotation task with a new control task designed to tax visuospatial working memory (Fig 1). Here, a sequence of circles was presented on a visual ring, and after a delay period a probe stimulus was displayed, where the position of the probe matched the position of one of the previously viewed circles. 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 set size imposed on spatial working memory. If the dissociation observed in Exp 1a is related to the spatial processing demands associated with mental rotation rather than the continuous nature of the required mental transformation, we would expect to observe an increase in slope in the CD group relative to the control participants on both the mental rotation task and the spatial working memory search task. However, if the dissociation described in Exp 1a is replicated, Exp 1b would provide further support for the CoRT hypothesis.

14 participants with CD and 14 control participants were tested in Exp 1b, none of whom had participated in Exp 1a. Moreover, we opted to use years of education as a second proxy for providing a crude index of cognitive ability, to complement the MoCA scores.

RT effects

RT slopes were positive for both groups in the mental rotation and working memory search tasks (Fig 4; all p's$_{perm} < 0.001$). Thus, rotation size and set size induced an increase in RT in both groups. Similar to Exp 1a, RT intercepts estimated from the mental rotation data were significantly higher in the CD group compared to the Controls ($p_{perm} = 0.002$; CD = 1097 $\pm$ 324 ms; Control = 1007 $\pm$ 283 ms), and marginally higher in the CD group in the estimates from the memory search data ($p_{perm} = 0.06$). RTs for the CD group were markedly slower than the Controls, even for the smallest set size ($p_{perm} = 0.02$).

Critically, we replicated the between-group slope difference on the mental rotation task: There was a main effect of group, with the CD group showing a higher slope compared to the control group ($F_{(1, 24)} = 6.8$, $p = 0.03$, Fig 4a, b). This difference was also observed in the direct two-sample permutation test ($p_{\text{perm}} = 0.03$). Mental rotation slopes were not affected by age ($F_{(1, 24)} = 0$, $p = 0.9$) nor baseline RTs ($F_{(1, 24)} = 0.7$, $p = 0.4$). The rotation rates were similar to that observed in Exp 1a with this new sample, with mean rates of 2.4 ms/deg for the Control group and 3.5 ms/deg for the CD group. A post-hoc, between-experiment comparison of the mental rotation slopes showed no difference in both CD groups ($t_{(24)} = 0.09$, $p = 0.9$; JZS Bayes Factor = 3.57 in favor of the null) and Control groups ($t_{(24)} = -0.18$, $p = 0.9$; JZS Bayes Factor = 3.53 in favor of the null), signaling a successful replication.

In contrast to the mental rotation task, there was no group effect of slope in the spatial memory search task, either when analyzed with the ANCOVA ($F_{(1, 24)} = 0.1$, $p = 0.80$, Fig 4c, d) or the direct two-sample permutation test ($p_{\text{perm}} = 0.85$). That is, the CD group did not exhibit an increase in terms of the time required to search through a discrete set of spatial locations in working memory. Slopes were not affected by age ($F_{(1, 24)} = 0.4$, $p = 0.56$), but were influenced by baseline RTs ($F_{(1, 24)} = 12.1$, $p = 0.002$).

In a direct comparison of the rate measures between the two tasks, the CD group showed a significantly larger increase in slope on the mental rotation tasks in comparison to the visuospatial memory search task (task X group interaction: $d_{Rotation} - d_{Search} = 1.45$, $p_{perm} < 0.001$). In summary, the RT data replicate the dissociation observed in Exp 1a: Degeneration of the cerebellum was selectively associated with a slower rate on a task that required a continuous transformation, but not on a task that involved an iterative search over a set of discrete representations. Furthermore, this dissociation is at odds with the alternative hypothesis that the cerebellum's involvement in visual cognition is related solely to spatial demands of the task.

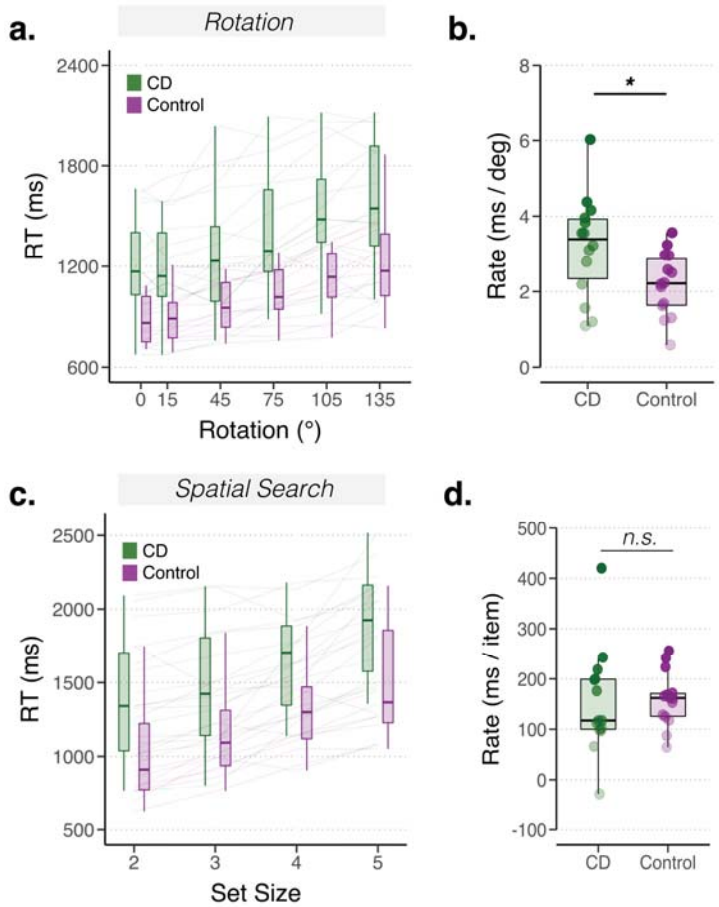

Figure 4: Reaction time analysis for Exp 1b. *Impairment in manipulation of spatial information is found for mental rotation, but not search through spatial working memory.* In a replication of Exp 1a, **(a-b)**, CD group (green) showed slower mental rotation speeds relative to controls (purple). Mental rotation rates are plotted with the absolute rotation magnitude of the stimulus on the x-axis, and the median 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 (set size) is plotted on the x-axis, and the median change in RTs for each set size on the y-axis. Thin lines denote individual data in panels **(a)** and **(c)**. Box and whisker plots delineate the median, 1st/3rd quartile, and max/min. * $p < 0.05$.

Accuracy effects

In terms of accuracy (Fig 5), 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 this difference may reflect differences in task difficulty, it is important to note that the number of response options differ between 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 set size). Unlike Exp 1a, accuracy scores were not significantly different between the CD and Control groups on the mental rotation task ($F_{(1, 24)} = 0.3$, $p = 0.57$). However, the CD

group performed significantly worse in the memory search task ($F_{(1,\ 24)}$ = 5.0, p = 0.04), consistent with previous findings (Molinari et al., 2004). Accuracy on both tasks was neither affected by age (rotation: $F_{(1,\ 24)}$ = 0.8, p = 0.4; search: $F_{(1,\ 24)}$ = 0.03, p = 0.87) nor baseline RT (rotation: $F_{(1,\ 24)}$ = 0.2 p = 0.66; search: $F_{(1,\ 24)}$ = 0.5, p = 0.48).

As in Exp 1a, we asked if the slope differences might reflect a speed-accuracy tradeoff (Fig 5b, c). As expected, the functions relating rotation magnitude and set size to task accuracy were negative. However, the slope of these functions did not differ significantly between groups (rotation; p_{perm} = 0.74; search; p_{perm} = 0.97; task X group interaction: $d_{Rotation} - d_{Search} = 0.15,\ p_{perm} = 0.44$).

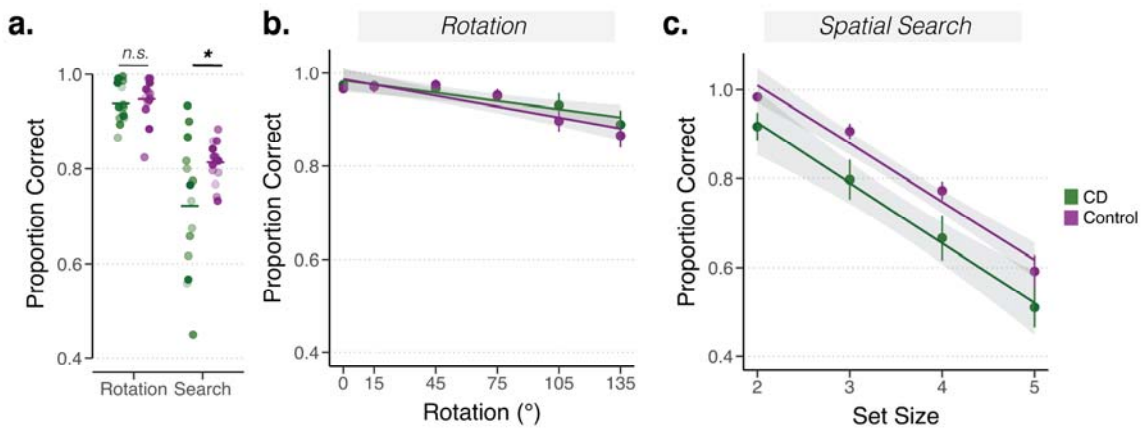

Figure 5: Accuracy analysis for Exp 1b. *Accuracy is a function of rotation angle and memory load, with group difference only observed on the search task.* **(a)** Overall accuracy rate is lower for CD group compared to Controls on the visuospatial working memory task (dots are shaded according to the within-group ranking of mental rotation and search paces, as seen in Figs 4b and 4d, with the darkest shade denoting the slowest rate and the lightest shade denoting the fastest rate; horizontal line indicates group means). Effects of independent task variables (rotation magnitude in panel **(b)** and set size in panel **(c)**) could not explain group differences. Error bars = 1 s.e.m. * p < 0.05.

Experiment 2: Assessing CoRT in the Domain of Mathematical Cognition

The results of Exps 1a and 1b are consistent with the CoRT hypothesis, with the selective impairment on the rate of mental rotation assumed to reflect the involvement of the cerebellum in transforming the orientation of the stimulus to facilitate perceptual decision-making. Importantly, there was no impairment in the CD group in processing rates for both the non-spatial and spatial retrieval tasks, arguing against a more generalized impairment. To further test the generality of the CoRT hypothesis, we turned to a markedly different domain in Exp 2: mental arithmetic.

As noted in the *Introduction*, a large body of literature presents a contrast between algorithmic and memory retrieval processes involved in simple arithmetic (Dehaene, 1999; Dehaene & Cohen, 1997; Fayol & Thevenot, 2012). In particular, adding single digits is hypothesized to involve the transformation of spatialized mental representations along a mental number line. Given various magnitude effects observed in addition problems (Restle, 1970), these transformations have been hypothesized to occur in a continuous manner; for example, verifying that 5 + 4 = 9 entails traversing a distance of four units along a number line. Given this assumption, we predicted that individuals with CD would be slower in performing such calculations; specifically, that they would show an elevated magnitude effect such that the RT difference between the CD and Control group would become larger with the magnitude of the operands (or sum). To test whether this effect is particular to continuous transformations, we included arithmetic tasks associated with memory retrieval from a discretized look-up table.

Experiment 2a

Participants included 15 individuals with CD and 15 Control participants. We used a verification task in which the participants made a speeded response to indicate if addition equations composed of two single-digit operands and a sum were true or false (Fig 6). The operands were between 3 and 8 and included all pairwise combinations and orders. Unlike Experiment 1, the CoRT and non-CoRT conditions here involved the same task: The CoRT condition was composed of trials in which the two operands were non-identical (e.g., 5 + 8), problems that are presumed to be solved with a mental number line, while the non-CoRT condition was composed of trials in which the two operands were identical (e.g., 6 + 6), problems presumed to be relatively automatized and solved via memory retrieval (Groen &

Parkman, 1972). The participants completed a single block that included 230 non-identical trials and 46 identical trials, with the presented equation being true in half of the trials and false in the other half.

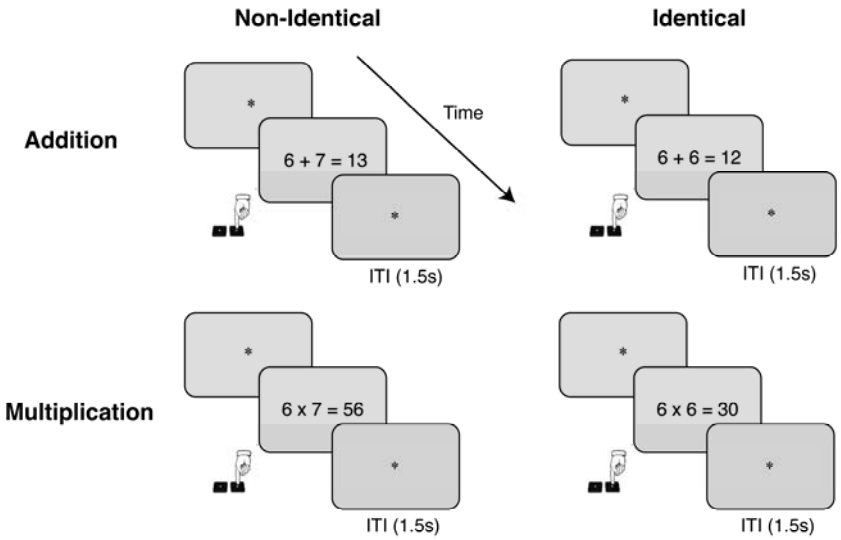

Figure 6: Task progression for Exp 2a and 2b. *Arithmetic Tasks.* Participants made a speeded response to verify whether the equation was true or false. Addition problems (top row, tested in Exp 2a and 2b) and multiplication problems (bottom row, tested in only Exp 2b) involved either non-identical operands (left column) or identical operands (right column). Non-identical addition constitutes the only CoRT condition, whereas the remaining three constitute non-CoRT conditions.

RT Effects

In contrast to Exp 1, the independent variable (operationalized as the max operand, see Methods) was identical for the CoRT and non-CoRT conditions. As such, we were able to use linear mixed effects modeling to analyze both within-participant and between-participant fixed effects.

The mean RT for the CD group was ~300 ms slower than for the Control group, although this effect was not statistically significant due to considerable individual differences (Fig 7a & c; $\chi^2(1) = 6.3,\ p = 0.15$; CD = 1330 $\pm$ 207 ms; Control = 1135 $\pm$ 112 ms). The main effect of problem type (i.e., identical versus non-identical) was not significant, ($\chi^2(1) = 0.4,\ p = 0.55$), indicating that evaluating equations with identical and non-identical operands required comparable processing times. There was no interaction between group and problem type

($\chi^2(1) = 1.2,\ p = 0.27$). Thus, the RT advantage for the Controls was similar in the two conditions.

Our main focus is on the change in RT that occurs as a function of the max operand. There was a marginal main effect of max operand, with RT increasing with the max operand ($\chi^2(1) = 3.0,\ p = 0.08$). There was an interaction between problem type and max operand ($\chi^2(1) = 11.9,\ p < 0.001$) (Fig 7a & c): Whereas RT increased with max operand for the non-identical equations, it was essentially flat for identical equations, consistent with previous studies (Groen & Parkman, 1972). Critically, this effect was modulated by the group factor as indicated by the significant three-way interaction between the factors group, problem type, and max operand ($\chi^2(1) = 6.3,\ p = 0.01$).

To analyze this three-way interaction, we estimated each individual's RT slope using linear regression, similar to the procedure employed in Exp 1. Based on a direct permutation test, RT slopes when adding different operands were found to be substantially larger in the CD group compared to Controls (Fig 7a; p_{perm} = 0.008). On average, individuals with CD required an additional ~150 ms per increment along the putative number line, whereas Controls only required an additional ~25 ms for each increment. In contrast, RT slopes for equations involving identical operands were similar between groups (Fig 7c; p_{perm} = 0.12). Taken together, these results point to a selective impairment for the CD group on the putative CoRT equations rather than a general deficit in arithmetic.

Age and baseline RTs were included as covariates in the mixed effect model. RT slopes were not affected by age ($\chi^2(1) < 0.01,\ p = 0.99$) but were influenced by baseline RTs ($\chi^2(1) = 1.0,\ p = 0.002$), as seen in Experiment 1. Slower baseline RTs were associated with steeper slopes, and this effect was similar for both the CD and Control groups.

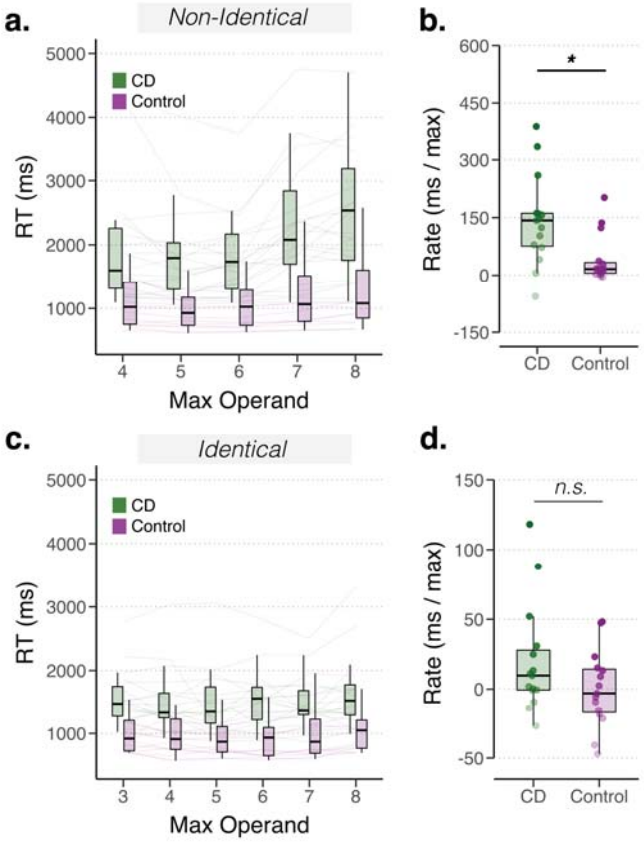

Figure 7: Reaction time analysis for Exp 2a. *Cerebellar degeneration associated with slower rate for addition problems putatively linked to transformations along a mental number line, but not problems assumed to depend on memory retrieval.* Median RT is plotted as a function of the maximum operand for equations with non-identical **(a)** and identical operands **(c)**. Thin lines denote functions for each participant. The rate of adding non-identical **(c)** or identical operands **(d)**, is estimated by the slope of each individual's RT function. Dots denote individuals. Box and whisker plots delineate the median, 1st/3rd quartile, and max/min. * $p < 0.05$.

Accuracy Effects

As shown in Fig 8a, accuracy was high for both non-identical (94.77%, SD = 4.07) and identical equations (97.24%, SD = 3.40). The two groups performed equally well ($\chi^2(1) = 0.2$, $p = 0.66$), with all individuals performing above 80% on both problem types (Figs 8a-c). There was a marginal effect of max operand on accuracy ($\chi^2(1) = 3.2$, $p = 0.07$), with accuracy tending to fall off with larger operands (Groen & Parkman, 1972). This fall-off was similar for both groups ($\chi^2(1) = 0.2$, $p = 0.70$), evidenced by the near-parallel lines seen in Figs 8b & 8c. Because the size of the operand had a similar effect on performance in both groups, a speed-

accuracy trade-off did not provide a parsimonious account for the RT results. Finally, there was neither an effect of age ($\chi^2(1) = 1.54,\ p = 0.22$) nor baseline RTs ($\chi^2(1) = 0.17,\ p = 0.68$) on accuracy.

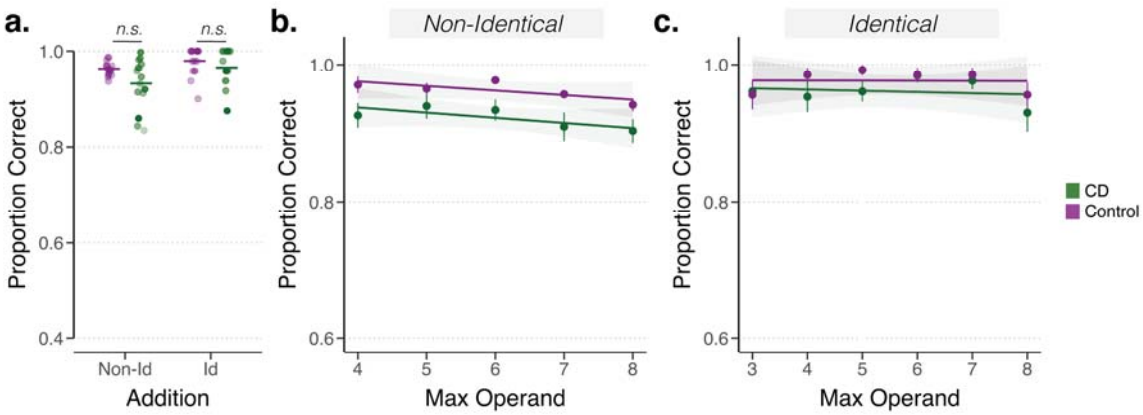

Figure 8: Accuracy analysis for Exp 2a. *Accuracy is comparable for the CD and Control groups in Exp 2a and does not provide evidence of a speed-accuracy tradeoff.* Overall performance **(a)** for each individual (dots) for the two types of addition problems (non-identical vs identical). Dots are shaded according to the within-group ranking of RT slopes, as seen in Figs 7b and 7d, with the darkest shade denoting the slowest rate and the lightest shade denoting the fastest rate; horizontal line indicates group means. Accuracy as a function of the maximum operand for equations with non-identical **(b)** and identical operands **(c)**. Mean regression lines are displayed in **(b)** and **(c)**. Error bars = 1 s.e.m.

Experiment 2b

Equations involving identical numbers were selected as the control (non-CoRT) condition in Experiment 2a given prior evidence showing that such over-trained problems are generally solved via memory retrieval (Groen & Parkman, 1972), a process that presumably does not involve a continuous transformation along a number line. While this meets the criterion for a non-CoRT condition, there are other differences between the two problem types: First, having identical operands might facilitate encoding of the equations, speeding decision-making. Second, and more importantly, identical operands did not elicit a parametric RT increase with the max operand. As such, this condition renders the rate measure difficult to interpret, since the time required for that operation is essentially invariant for all of the equations with identical operands (e.g., RT is the same for 2 + 2 and 6 + 6).

In Exp 2b we address these limitations by comparing addition to multiplication, using the same set of operands for both tasks. The time required to perform and verify multiplication problems involving two single-digit numbers increases with the max operand, as in non-identical

addition problems (LeFevre et al., 1996). However, the magnitude effect for multiplication has been associated with differences in the time required to access a look-up table, an effect related to the associative strength between operands and their solution, likely mediated by experienced problem frequency (Campbell & Graham, 1985; Miller et al., 1984). Thus, based on the CoRT hypothesis, we expected that the CD group would show an increase in slope for the addition problems, replicating Exp 2a, but not for the multiplication problems. An added feature of comparing addition and multiplication is that, *a priori*, we assumed that multiplying two single-digit numbers is more difficult than adding the same numbers. Thus, an impairment associated with CD is here predicted for the putatively easier condition.

15 individuals with CD and 15 Controls were tested in Exp 2b (12 CD and 7 Controls were also tested in Exp 1b—see *Methods*). To eliminate switching costs between operations, addition and multiplication were tested in separate blocks of 288 trials each, with task order counterbalanced. The set of operands was slightly different than that used in Exp 2a, now including numbers ranging from 3 to 9. We replaced 5 with 9 in Exp 2b given concerns that multiplying by 5 could be easier than other two-digit multiplication problems. Since CoRT equations involved addition equations consisting of only non-identical operands, RT performance on these equations were contrasted with non-CoRT equations that involved multiplying the same non-identical operands.

RT Effects

We first consider the addition and multiplication equations with non-identical operands. The mean RT for the CD group was slower by ~300 ms relative to the Control group ($\chi^2(1) = 38,\ p < 0.001$; CD = 1583 $\pm$ 114 ms; Control = 1113 $\pm$ 74 ms), similar to that observed in Exps 1a, 1b, and 2a. The main effect of problem type on RT was not significant ($\chi^2(1) = 1.7$, $p = 0.19$). RTs increased robustly with the max operand (main effect of max operand: $\chi^2(1) = 23.2,\ p < 0.001$), exhibiting an incremental RT cost of ~40 ms per max operand for both problem types (problem type X max operand interaction not significant: $\chi^2(1) = 1.9, = 0.17$).

Consistent with the CoRT hypothesis, there was a significant three-way interaction of group, problem type, and max operand ($\chi^2(1) = 27.5,\ p < 0.001$): The increase in RT with increasing max operands was larger for the CD group compared to the Controls, but only for the addition condition (Fig 9a; $p_{\text{perm}} = 0.011$). Whereas the CD group required an additional ~65 ms

for each integer increment in the max operand, the comparable value for the Controls was only ~23 ms/integer. We note that the control group rate in Exp 2b was comparable to that observed for addition with non-identical equations in Exp 2a, although the rate for the CD group was considerably faster in Exp 2b (~150 ms). Nonetheless, the larger value for the CD group, compared to the control group, is consistent with our prediction.

In contrast to addition, the RT slopes estimated from the multiplication condition were comparable for the two groups (Fig 9c; $p_{\text{perm}} = 0.42$). If expressed in the units used for addition, the mean rate values were 55 ms/integer and 48 ms/integer for the CD and Control groups, respectively. Importantly, the current results indicate that this putative memory retrieval process is unaffected by cerebellar degeneration, also consistent with the results of the non-CoRT condition in Exp 2a.

Finally, to evaluate whether other covariates had an effect on RT, we included age and baseline RTs in the mixed effects model. We observed neither a significant effect of age ($\chi^2(1) = 0.4,\ p = 0.46$) nor a significant effect of years of education ($\chi^2(1) = 4.7,\ p = 0.06$), suggesting that the group differences in RT were primarily driven by cerebellar pathology.

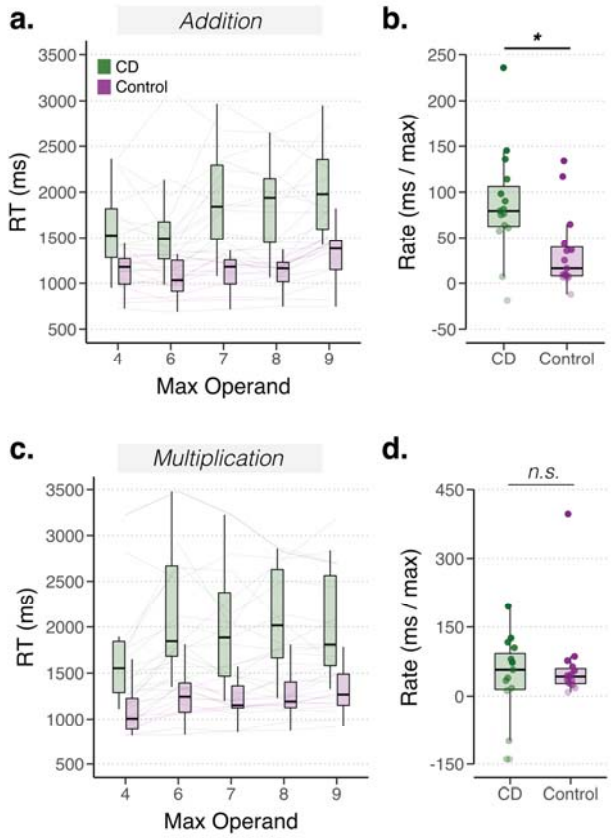

Figure 9: Reaction time analysis for Exp 2b. *Replication of selective impairment in CD group on arithmetic problems associated with number line transformations.* Median RT is plotted as a function of the maximum operand for addition **(a)** and multiplication **(c)**, using equations with non-identical operands only. Thin lines denote functions for each participant. The rate for addition **(c)** or multiplication **(d)**, is estimated by the slope of each individual's RT function. Dots denote individuals. Box and whisker plots delineate the median, 1st/3rd quartile, and max/min. * p < 0.05.

Accuracy Effects

As predicted, there was a significant main effect of problem type on accuracy ($\chi^2(1) = 11.6,\ p < 0.001$), where accuracy (Fig 10) was lower on the multiplication problems (91.70%, SD = 5.52) compared to the addition problems (95.54%, SD = 0.03). While there was no main effect of the max operand on accuracy ($\chi^2(1) = 2.19,\ p = 0.13$), this variable interacted with problem type ($\chi^2(1) = 30.39,\ p < 0.001$), with accuracy declining at a faster rate for multiplication compared to addition (Figs 10b, 10c).

We again asked whether the RT effects might be mitigated by group differences in speed-accuracy tradeoffs. There was a significant three-way interaction in the accuracy data of max operand, group, and problem type ($\chi^2(1) = 5.52,\ p = 0.02$). Accuracy decreased faster as a

function of max operand on multiplication problems for the CD group compared to the Controls, whereas the accuracy decrease with max operand was similar for the two groups on addition problems (multiplication: $p_{perm} = 0.03$; addition: $p_{perm} = 0.87$). This interaction could indicate that RT differences between groups for multiplication were masked by accuracy differences. We thus examined the relationship between the slope values for the accuracy and RT data: If participants were trading speed for accuracy, then a larger change in accuracy with max operand should be associated with a smaller change in RT with the max operand, and vice-versa. This correlation was neither observed for the Control group (multiplication: $r = 0.03,\ p = 0.93$; addition: $r = 0.12,\ p = 0.7$) nor the CD group (multiplication: $r = 0.15,\ p = 0.56$; addition: $r = 0.4,\ p = 0.1$), arguing against a speed accuracy account for the null effects observed in the multiplication RT slopes.

In terms of covariates, there was no effect of age on accuracy ($\chi^2(1) < 0.01,\ p = 1$); however, there was an effect of baseline RT ($\chi^2(1) = 13,\ p < 0.001$). As observed previously, slower baseline RTs were associated with steeper slopes, and this effect was similar for the two groups.

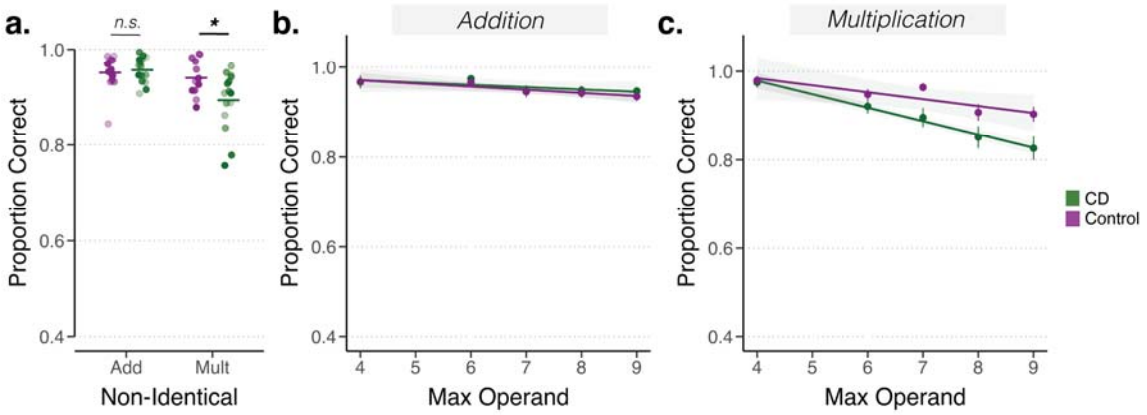

Figure 10: Accuracy analysis for Exp 1a. *Accuracy is comparable for the CD and Control groups in Exp 2b and does not provide evidence of a speed-accuracy tradeoff.* Overall performance **(a)** for each individual (dots) for addition and multiplication problems consisting of non-identical operands. Dots are shaded according to the within-group ranking of RT slopes, as seen in Figs 9b and 9d, with the darkest shade denoting the slowest rate and the lightest shade denoting the fastest rate; horizontal line indicates group means. Accuracy as a function of the maximum operand for non-identical addition **(b)** and multiplication equations **(c)**. Mean regression lines are displayed in **(b)** and **(c)**. Error bars = 1 s.e.m.

Comparison of problems with identical operands

While our main hypothesis centered on the comparison of addition and multiplication equations with non-identical operands, the addition and multiplication conditions both included equations with identical operands. Similar to that observed in Exp 2a for the addition problems with identical operands, the functions for both groups with both types of equations were essentially flat. There was a main effect of group ($\chi^2(1) = 17.1,\ p < 0.001$), but no group X max operand interaction ($\chi^2(1) < 0.1,\ p = 1$). We directly extracted RT slopes using linear regression and compared these values between groups for each task. RT slopes were not significantly different between groups for addition with identical operands (Fig 11b: $p_{perm} = 0.97$) and multiplication with identical operands (Fig 11e: $p_{perm} = 0.33$). These results provide further evidence that cerebellar degeneration does not impact the speed of memory retrieval. Accuracy was relatively high in both tasks (Fig 11c & 11f), and again, the observed functions did not suggest an elevated cost for the CD group for larger operands when the presented pair were identical.

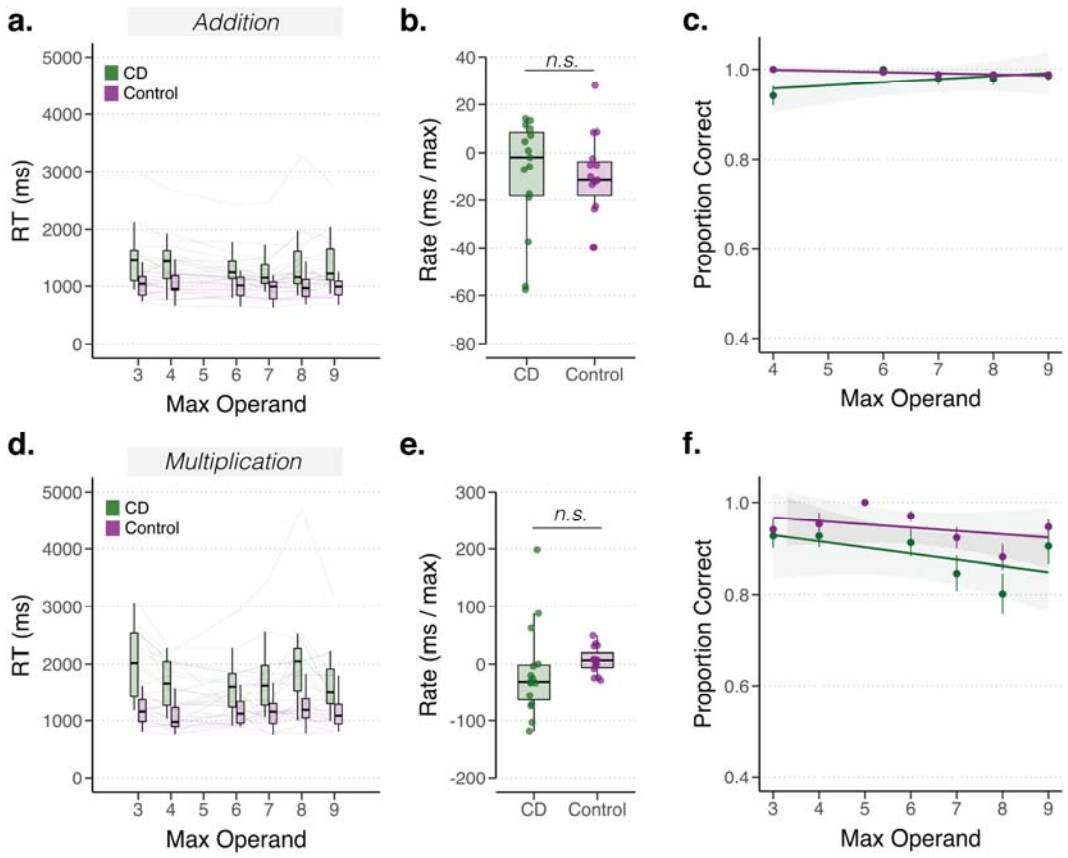

Figure 11: Secondary reaction time analysis for Exp 2b. *Memory retrieval from a look-up table is spared in CD*. Median RT as a function of the maximum operand in computing **(a)** addition equations with identical operands and **(d)** multiplication equations with identical operands. The CD group is shown in green, and the control group in purple. Thin lines denote individuals. The rate of adding **(b)** and multiplying identical operands **(e)** is estimated by extracting the slope of each individual's median RTs. Dots denote individuals. Mean proportion correct as a function of the maximum operand for **(c)** addition with identical operands and **(d)** multiplication with identical operands. Mean regression lines are displayed in **(c)** and **(f)**. Box and whisker plots delineate the median, 1st/3rd quartile, and max/min. Error bars = 1 s.e.m.

DISCUSSION

The cerebellum is a major anatomical 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 the role of the cerebellum in cognition has remained limited. 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). Alternatively, the homogeneous anatomy and physiology of the cerebellum has inspired the idea that the cerebellum may invoke a common computation across diverse task domains (Diedrichsen et al., 2019; Schmahmann et al., 2019), or what has been called a "universal cerebellar transform" (UCT). By this view, the functional diversity inferred from the neuroimaging literature is seen as reflecting the diversity of inputs to the human cerebellum (Lauritzen, 2001), with a UCT being applied to these inputs to support a range of behaviors.

While recognizing that homogenous structure and physiology need not imply homogenous function, the UCT concept has been useful in generating testable computational hypotheses (Allen et al., 1997; Ito, 2008; Ivry & Keele, 1989; Miall et al., 1993; Wolpert et al., 1998). Here we build on this concept, seeking to identify constraints on the type of cognitive operations that rely on the cerebellum. Inspired by the cerebellum's role in motor coordination, we propose one such constraint – that the cerebellum facilitates processing in tasks that involve a continuous representational transformation. Continuous and discrete operations reflect a key dimension for describing mental transformations (Miller, 1988). For motor control, the dynamics required to efficiently manipulate a physical object, the body and its interactions with the environment, are continuous. This continuity is disrupted in cerebellar ataxia – the individual is able to generate the appropriate motor plan, but the execution becomes disjointed, failing to show the smooth continuous transition between states that is the hallmark of coordinated movement. The CoRT hypothesis extends this continuity constraint, pointing to an algorithmic account of how the cerebellum may help facilitate the efficient, or coordinated operation of nonmotor mental operations. The hypothesis can thus be used to generate specific predictions about which cognitive processes are likely to be most impacted by cerebellar dysfunction.

As an initial testbed of the CoRT hypothesis, we focused on visuospatial cognition, comparing two classes of visuospatial cognition tasks, one shown to be highly dependent on a continuous mental transformation (mental rotation) and the other associated with putatively more discrete operations (iterative search through items in working memory). Reaction time slopes, taken as a proxy for the core mental operation required in these tasks, were elevated in the cerebellar degeneration group for mental rotation but not for visual (Experiment 1a) or visuospatial (Experiment 1b) working memory search. We note that this dissociation was

observed in two independent samples of individuals with cerebellar degeneration (CD) and matched controls.

To assess the generality of the CoRT hypothesis, we turned to a second task domain, mathematical cognition (Experiments 2a and 2b). In these tasks, operations such as simple addition are thought to rely on translations across an internal spatialized representation of a number line, with this representation imposing constraints on processing speed for transformations within this space. Other operations such as addition of identical single-digit integers or multiplication are thought to rely on rote retrieval of instances from memory (e.g., 2 x 2), or simple algorithmic recipes (e.g., 10 x 63). Consistent with the CoRT hypothesis, individuals with CD were selectively impaired on the problems involving a mental number line, manifest as a larger increase in RT with operand magnitude. In contrast, their RT slopes were similar to the Controls on the two arithmetic tasks thought to be dependent on retrieval from a look-up table. As in Experiment 1, this dissociation was observed in two independent samples of participants. Taken together, these findings point to a functional role for the cerebellum in visual and mathematical cognition, and suggest that this role may be specifically suited to facilitating processing when the tasks require continuous representational transformation.

As noted above, the CoRT hypothesis is inspired by previous theoretical conjectures that take as their starting point cerebellar computations for motor control and generalize those 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 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 in my mind? Similarly, traversal of a mental number line would require an analogous state transition from one point in mental space to another (e.g., from left to right). To date, an extension of the internal model idea to cerebellar cognitive function has emphasized manipulation and prediction in a general sense. On such a general account, any manipulation of information in working memory could fall within the functional domain of the cerebellum. The current findings suggest a more specific role for the cerebellum in cognitive processes, those that rely on continuous mental transformations. By this view, the CoRT

hypothesis shifts the focus away from an singular emphasis on prediction *per se*, and more towards consideration of the particular type of transformation required for certain predictions.

We also note here that the results from Experiment 1 may provide a novel 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). It has recently been 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). Curiously, their impairment was manifest "under-aiming", that is, choosing a strategy that failed to fully compensate for the perturbation. When viewed within the context of the CoRT hypothesis, this pattern would suggest that the impairment is not some sort of generic problem in strategy use but arises because this form of aiming requires mental rotation. That is, an initial movement plan is directed at the target and then parametrically rotated to produce the desired outcome (Georgopoulos & Pellizzer, 1995; McDougle & Taylor, 2019). Accordingly, the under-aiming observed in the CD group could reflect an impairment in mental rotation. That is, a slower mental rotation rate with a (roughly) unchanged decision bound would result in under-aiming.

In contrast, it has been argued that the aiming deficit in CD groups could be interpreted as an attentional problem, where failing to adapt diverts attention to the persistent error and reduces resources available for strategy use. In support of this attentional account, the aiming deficit in a CD sample was attenuated when the task was made easier by enhancing the feedback (Wong et al., 2019). This would appear at odds with our CoRT-based interpretation of the aiming impairment, since aiming should rely on mental rotation independent of the attentional load. While there are a number of significant methodological differences between the Butcher et al. (Butcher et al., 2017) and Wong et al. (Wong et al., 2019) studies, one notable difference is that the latter used only four target locations. With only a few target locations, neurologically-intact individuals appear to "cache" stimulus-response associations between targets and movements (McDougle & Taylor, 2019), converting an algorithmic-based process (i.e., mental rotation) into

a retrieval process. Thus, the preserved “strategy use” in the CD group in the Wong et al. (Wong et al., 2019) study may not be indicative of the generic effects of an attentional load manipulation, but rather their use of conditions that putatively favored a non-CoRT operation for strategic aiming.

One open question concerns observed group differences not accounted for by the CoRT 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 global motor deficits associated with CD. However, baseline RT differences between the CD and control groups were around ~320 ms across the two mental rotation tasks and ~470 ms across the two working memory search tasks, values considerably larger than those observed in tasks involving relatively simple perceptual discriminations (e.g., Breska & Ivry, 2018). Second, although not dependent on set size, the CD group had worse accuracy than the control group on the mental rotation task in Experiment 1a and on both of the memory search tasks (Figs 3a, 5a). Taken together, these results suggest that, in addition to a specific impairment on the putative CoRT-dependent operation, the CD participants likely also have more generic impairments that influenced behavior in the tasks used here.

A second limitation centers on the group differences in accuracy observed in the multiplication task (Experiment 2b), a deficit that became more pronounced as the operand increased. While this observation seems at odds with the CoRT hypothesis, given the assumption that multiplication relies on memory retrieval (LeFevre et al., 1996), we posit that these deficits in accuracy may reflect a more generic effect of CD. We deliberately avoided the use of accuracy as our main dependent variable because this measure is likely to be sensitive to many cognitive processes: Poor accuracy may stem from attentional lapses, encoding errors, response biases, etc., and all these would be expected to increase with problem difficulty. In contrast, we selected tasks that allowed us to focus on parametric changes in RT (limited to correct trials), as this type of dependent variable provides a proxy of more specific cognitive processes (e.g., the rate of mental rotation, serial or parallel memory search, movement along a mental number line, etc.). We also note that in two of our experiments (Experiments 1a and 2b), the tasks in which we did not see a CD deficit in RT slopes were apparently the more difficult of the two tasks, arguing against a generic difficulty confound.

Although some neuropsychological studies have reported cognitive deficits in CD that are consistent with the CoRT hypothesis (e.g., Molinari et al., 2004), other studies have revealed impairments that appear to be inconsistent with (or unrelated to) this 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 CoRT hypothesis as a candidate UCT.

This last point underscores an important feature of the CoRT hypothesis as a UCT. By postulating a strong constraint on cerebellar cognitive computation – the distinction between continuous and discrete mental transformations – the hypothesis is readily falsifiable. Ideas about the cerebellum and cognition that focus on prediction or coordination of thought can be difficult to empirically test, the former being too general (much of brain function is predictive) and the latter too descriptive. We anticipate that it should be relatively straightforward to extend the CoRT hypothesis to other cognitive domains. For instance, some models of attention posit a covert "spotlight" that traverses the visual scene (Posner & Boies, 1971; Tsal, 1983). Speculatively, the continuous representational transformation hypothesis would predict that individuals with CD could be impaired at smoothly moving a putative attentional spotlight through space. Similarly, the involvement of the cerebellum in language may be restricted to linguistic or semantic operations that entail continuous representational transformations (and not those that involve discrete transformations). Future studies involving a broader range of cognitive tasks could further evaluate our proposal.

METHODS

Participants

Adult participants diagnosed with spinocerebellar ataxia due to cerebellar degeneration (N = 44) and neurologically healthy controls (N = 42) participated in the study in exchange for monetary compensation ($20 per hour). All of the participants were screened for general cognitive deficits using the Montreal Cognitive Assessment. Inclusion required that the participant achieve a score above 20 on the 30-point scale. 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), ranging from 2 (mild motor impairments) to 26 (severe motor impairments). In most cases, the diagnosis was confirmed from a combination of family history, genetic profiling, and MRI scans. 22 of the 44 individuals with ataxia had an identified subtype (SC1: 4; SCA3: 4; SCA5: 1; SCA6: 8; SCA8: 1; SCA15: 1; SCA28: 1; AOA2: 2); for the other individuals, genetic testing was inconclusive or absent. The 8 CD participants with confirmed SCA6 were all related.

Control participants were, in general, well-matched to the clinical sample in terms of age, MoCA, and years of education (see Table 1). The one exception was in Exp 1b; by emphasizing matches based on education in this study, we ended up with a CD sample that was significantly older than their control group. Given this difference, we included age as a covariate in the primary analyses of all of the experiments (see below).

The test session last approximately 2 hours, including time for obtaining consent, medical history, performing the neuropsychological (all) and neurological (for CD only) evaluations, conducting the experimental tasks, and multiple breaks. A test session included two different experimental tasks. A subset of the participants (CD =12; Controls = 7) completed two of the tasks reported here Exps 1b and 2b) in a single session. For the other participants, the second task focused on sensorimotor learning.

	Age		MoCA		Years of Education		Sex		SARA
	CD	**Control**	**CD**	**Control**	**CD**	**Control**	**CD**	**Control**	**CD**
Exp. 1a	49.8 (37 – 70)	50.2 (35 – 68)	28 (26 – 29)	29 (27 – 30)	Not collected		5 F 7 M	5 F 7 M	11.8 (5 – 22)
Exp. 1b	57.2* (32 – 71)	50.7* (33 – 73)	27 (22 – 29)	25 (21 – 28)	15.8 (12 – 22)	16.4 (13 – 20)	11 F 3 M	10 F 4 M	11.3 (2 – 25)
Exp. 2a	53.3 (33 – 68)	56.5 (32 – 74)	27 (20 – 30)	28 (25 – 30)	16.9 (12 – 24)	17.7 (16 – 22)	10 F 5 M	7 F 8 M	13.7 (5 – 26)
Exp. 2b	56.5 (32 – 77)	58.3 (34 – 73)	26 (21 – 30)	26 (23 – 29)	15.4 (12 – 20)	16.9 (15 – 20)	11 F 4 M	11 F 4 M	11.5 (2 – 26)

Table 1: *Demographic summary of CD and Control participants across all four experiments. Asterisks (*) denotes a significant difference ($p < 0.05$) between groups.*

Apparatus and Procedure Overview

For all experiments, the stimuli were displayed and responses recorded on a laptop computer (MacBook Pro, Apple), using the psychophysics toolbox package (Brainard, 1997) for MATLAB (MathWorks). Participants were seated a comfortable distance from the screen (viewing distance ~40 cm) and responded with their right hand which was positioned over the computer keyboard.

Experiments 1a and 1b were designed to evaluate the CoRT hypothesis in the domain of visual cognition. Each involved two conditions, an experimental condition hypothesized to entail a CoRT operation and a control non-CoRT condition. In both Exps 1a and 1b, the same mental rotation task was used for the CoRT condition. It was paired with a visual working memory task in Exp 1a and a visuospatial working memory task in Exp 1b. The CoRT and non-CoRT conditions were tested in separate experimental blocks within a single session, with the order counterbalanced. Each task took approximately 25 min to complete and participants were given a 10 min break between conditions.

Experiments 2a and 2b evaluated the CoRT hypothesis in the domain of mathematical cognition. Exp 2a consisted of only addition problems where the CoRT condition was composed of equations in which the two operands were non-identical and the non-CoRT condition was composed of equations in which the two operands were identical. These two types of equations were intermixed in a single block of trials that took approximately 25 min to complete. Both addition and multiplication problems were tested in Exp 2b, with the latter providing a second

non-CoRT condition. To minimize task-switching costs, the two types of operations were tested in separate blocks, each lasting approximately 25 min (plus the 10 min break), with the order counterbalanced across individuals.

Experimental Tasks

Exps 1a and 1b: Mental Rotation

Following the basic design of Shephard and Metzler (1971), participants judged if a visual stimulus was normal ("R") or mirror-reflected ("Я"; Fig 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 eye movements while maintaining stimulus legibility, the stimuli were modestly sized (~4 cm^2), of high contrast, and were presented at a central location on the monitor.

Participants were instructed to press the right arrow key with their right ring finger when the stimulus (if viewed or imagined in an upright orientation) was in standard form and the left arrow key with their right index finger if the stimulus was mirror reflected. The stimulus was presented in the standard upright orientation (0˚, baseline condition), or rotated, using one of 10 angles drawn from the following set: -135˚, -105˚, -75˚, -45˚, -15˚, 15˚, 45˚, 75˚, 105˚, 135˚. The stimulus remained visible until the response, or for a maximum of 5 s, whichever came first. After the response, feedback was shown above the letter 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, while maintaining a high level of accuracy. If no response was made within 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) that remained visible for a 2 s inter-trial interval.

Participants performed 18 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 random order, with an equal number of normal and reflected presentations of each stimulus 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.

Exp 1a: Visual Memory Search

As a non-CoRT control task in Exp 1a, we employed a variant of the "memory scanning" task introduced by Sternberg (1966). On each trial, participants viewed a brief sequence of visual stimuli and, after a maintenance period, judged 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).

The memory set was presented sequentially with each fractal image in the set displayed at the center of the screen for 1 s (with no inter-stimulus interval). To vary the working memory load across trials, the number of stimuli in a set ranged from 1 to 5 items. 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 the 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 set size were presented (10 match, 10 non-match) in a random order for a total of 100 trials. Participants completed five practice trials at the start of the experiment.

Exp 1b: Spatial Visual Memory Search

A spatial working memory task was employed for the non-CoRT condition in Exp 1b, adopted from a task introduced by Georgopoulos and Pellizzer (1995). On each trial, a sequence of red circles (diameter 1.2 cm) were displayed in succession on a white ring (radius 7 cm). A circle could be presented at any location from 0˚ - 345˚ (at multiples of 15˚), with the constraint that no location be repeated in a given sequence. Each stimulus was presented for 800 ms, with no time gap between successive targets. The number of stimuli in the sequence ranged from 2 to 5 items. Following the offset of the last item in the sequence, the white ring remained on the

screen for a maintenance period of 2 s, after which a probe stimulus was shown. The probe 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 if location of first item, “2” key if location of second item, etc.). 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 set size (i.e., sequence length, 2 - 5) was presented 30 times in a randomized order, for a total of 120 trials. Within each set-size, probe positions were sampled uniformly between the first and the second-to-last position; for example, if the set size was 5, the probe location could match the location of the first, second, third, or fourth target in the sequence. Except for a set size of 2, 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.

Exp 2a and 2b: Addition Verification

On each trial, participants indicated if an addition equation, composed of two single digit operands and a sum, was true or false (Groen & Parkman, (1972) (Fig 6). The CoRT condition consisted of trials in which the operands were non-identical (e.g., 4 + 7 = 11); the non-CoRT condition consisted of trials in which the operands were identical (e.g., 6 + 6 = 12). Equations were white and presented at the center of the screen on a grey background. To minimize the necessity of making large saccades while maintaining stimulus legibility, the total length of the equation was modestly sized (4 cm). The equations were presented in a standard format (e.g., 3 + 7 = 11) with a double digit always used for the sum (e.g., “09” if the indicated sum was 9) to reduce the use of heuristics (e.g., recognizing that 3 + 1 could not be a two-digit sum).

Equations were drawn from a set of 36 single digit equations. Equations in Exp 2a were comprised of all unique combinations of operands between 3 and 8. Equations in Exp 2b were comprised of all unique combinations of operands 3, 4, 6, 7, 8, 9. Operands less than 3 were removed to limit the number of combinations where magnitude effects were modest (Groen & Parkman, 1972). We also excluded the operand 9 in Exp 2a to further limit the number of combinations; we replaced the 5 with 9 in Exp 2b given concerns that multiplying by 5 (see non-CoRT control below) would be easier than other two-digit multiplication problems. Each

equation was presented eight times, consisting of four true responses and four false responses. True responses had one unique equation with the correct sum provided (e.g., 3 + 4 = 7). For the false equations, there were four distinct erroneous sums for each equation, with the presented answer different from the actual sum by either ± 1 (e.g., 3 + 4 = 8; 3 + 4 = 6) or ± 2 (e.g., 3 + 4 = 9; 3 + 4 = 5).

There was a total of 288 addition trials, with the equations with identical and non-identical operands randomly interleaved. The trial sequence was subject to three constraints to minimize the effects of numerical and response priming on reaction time (Sklar et al., 2012): 1) If answered correctly, the same response would not occur more than three times in succession; 2) Consecutive problems could not share identical operands; 3) Consecutive problems could not share the same solution. Note that this third constraint limits repetition of equations with the actual true solution, not the displayed solution, which could either be a true or false sum. The entire block took approximately 25 minutes.

Exp 2b: Multiplication Verification

Participants completed a second block of trials in Exp 2b in which they performed the verification task on multiplication equations. This condition was added to provide a second non-CoRT control condition given the assumption that participants use a look-up table in computing the product of two single-digit numbers (Campbell & Graham, 1985). The method for this condition was identical to that used in the addition block, including the use of the same set of operands (3, 4, 6, 7, 8, 9). Equations with erroneous products also had four variants, here created by adding ± 1 to either the first operand (e.g., 8 x 3 = 27 or 8 x 3 = 21) or ± 1 from the second operand (e.g., 8 x 3 = 16 or 8 x 3 = 32). There was a total of 288 trials consisting of equations with identical and non-identical operands, which were analyzed separately as in addition. The order of the addition and multiplication tasks in Exp 2b was counterbalanced across individuals.

Data Analyses

Trials associated with extreme outlier RTs (> ± 3.5 SD from the participant's mean) were removed prior to the analysis of the RT data. Less than 2% of trials were removed for all tasks. Parametric assumptions were tested using the Shapiro-Wilk test for normality and Levene's test for homogeneity of variance. When parametric assumptions were met (which was the case for

the accuracy data), statistical tests were performed on the mean values; when these assumptions were violated (which was the case for RT data for both groups in all experiments), non-parametric permutation tests were employed. All statistical tests were conducted in R (GNU).

Visual Cognition Tasks

The three tasks were selected because each has been shown to produce a parametric function relating the main independent variable, absolute rotation magnitude in mental rotation or set size in the two working memory search tasks, 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 distribution has been shown to better approximate RT distributions compared to the normal distribution (Lo & Andrews, 2015; McGill & Gibbon, 1965; Ratcliff, 1979).

Our hypothesis centered on the two-way interaction between group and task on RT slopes. Specifically, we predicted a larger slope for the CD group compared to the Controls on mental rotation, but no group difference on memory search. To directly compare group differences in RT slopes across tasks with different independent variables (degrees for mental rotation; set size for memory search), we first computed slope differences between groups for each task to obtain two effect sizes. We then took the difference between these two effects sizes and computed a p-value by comparing the actual difference in effect size against a permutation distribution obtained by shuffling group labels 1000 times. A p value less than 0.05 would indicate a disproportionate group difference in RT slopes for mental rotation versus memory search. Two-tailed permutation tests were used to compare group differences in RT slopes, with alpha set at 0.05 (non-parametric tests were used due to failure to meet parametric assumptions).

As a secondary analysis we compared differences in the RT slopes for each task separately. To this end, we performed an ANCOVA, with age and baseline median-centered RT included as covariates. The latter was motivated by the finding that the CD group was slower in responding across all tasks and conditions (baseline RT operationalized as rotation = 0˚ in mental rotation, set size = 1 in visual memory search, set size = 2 in spatial visual memory search).

Mathematical Cognition Tasks

With the exception of problems with identical operands, addition and multiplication verification tasks involving two single-digit operands have been shown to produce an increase in RT as a function of magnitude, with magnitude defined in a range of ways (max operand, min operand, first operand, second operand, or the solution) (Barrouillet & Thevenot, 2013; Groen & Parkman, 1972; Uittenhove et al., 2016). We opted to use max operand as the independent variable for both the addition and multiplication tasks in the present study, although the pattern of results remains unchanged when magnitude is operationalized with the four other definitions.

Unlike visual cognition, the same independent variable, max operand, applies across the mathematical cognition tasks. Therefore, performance on the CoRT and non-CoRT conditions could be directly compared using a linear mixed effect model. Raw RTs were entered into this linear mixed effect model (assuming gamma distributed residuals), with fixed effects consisting of the max operand, group, and problem type (Exp 2a: equations with identical vs non-identical operands; Exp 2b: equations with non-identical operands in addition vs non-identical operands in multiplication), and a random effect consisting of Participant ID. Our primary hypothesis centered on the three-way interaction among the fixed effects: Specifically, we predicted that the RT effect as function of max operand would be larger for the CD group only on the addition problems involving non-identical operands. This interaction was evaluated using a standard Chi-squared (χ^2) likelihood ratio test.

As in Exp 1a-b, we also performed a more conservative non-parametric permutation test to evaluate group differences in RT slopes. Here we again used an ANCOVA, allowing us to evaluate whether group differences in RT slopes were influenced by differences in age and/or baseline median-centered RT. For this measure, we opted to use the intercept from the regression analysis limited to the non-identical RT functions.

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