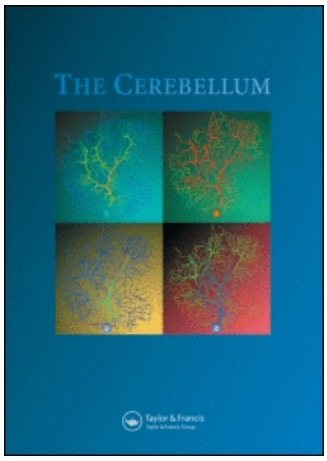

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ORIGINAL ARTICLE

Timing of rhythmic movements in patients with cerebellar degeneration

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Abstract
A distinction in temporal performance has been identified between two classes of rhythmic movements: those requiring explicit timing of salient events marking successive cycles, i.e., event timing, and continuous movements in which timing is hypothesized to be emergent. Converging evidence in support of this distinction is reviewed, including neuropsychological studies showing that individuals with cerebellar damage are selectively impaired on tasks requiring event timing (e.g., tapping). Recent behavioral evidence in neurologically healthy individuals suggests that for continuous movements (e.g., circle drawing), the initial cycle is marked by a transformation from event to emergent timing, allowing the participant to match their movement rate to an externally defined cycle duration. We report a new experiment in which individuals with cerebellar ataxia produced rhythmic tapping or circle drawing movements. Participants were either paced by a metronome or unpaced. Ataxics showed a disproportionate increase in temporal variability during tapping compared to circle drawing, although they were more variable than controls on both tasks. However, two predictions of the transformation hypothesis were not confirmed. First, the ataxics did not show a selective impairment on circle drawing during the initial cycles, a phase when we hypothesized event timing would be required to establish the movement rate. Second, the metronome did not increase variability of the performance of the ataxics. Taken together, these results provide further evidence that the integrity of the cerebellum is especially important for event timing, although our attempt to specify the relationship between event and emergent timing was not successful.

Key words: *Ataxia, timing, movement*

Introduction

Many models of cerebellar function emphasize a critical role for this structure in the representation of precise temporal information (1–4). These models seek to account for a range of task domains associated with the cerebellum, including the production of well-timed movements, certain types of sensorimotor learning, and various perceptual tasks in which precise timing is essential.

The production of rhythmic movements has been one of the most widely-employed tasks for studying timing. Rhythm production tasks are appealing for a variety of reasons. Analytically, formal models have been developed to differentiate between sources of variability (5,6). Methodologically, the required movements are sufficiently simple that they can be performed by participants with neurological disorders (7–9) as well as in the constrained environments used in neuroimaging research (e.g., 10,11). Studies using these models and methods have provided some of the foundational evidence in support of the hypothesis that the cerebellum operates as an internal timing system.

Our recent behavioral work with rhythmic movement tasks has led to a further refinement of the cerebellar timing hypothesis. In the original behavioral work, healthy college-aged participants did not show correlated individual differences on timing precision between tapping, a discrete task, and circle drawing, a smooth, continuous task (12–14). This dissociation led us to propose a distinction between event and emergent timing (15). In event timing, salient events such as the initiation point for each cycle or the point of contact with a surface (as in table tapping) define the temporal interval: the participant controls the timing of these events to match the task goal (e.g., maintain a movement rate defined by a metronome). In emergent timing, this goal may be achieved indirectly by exploiting the dynamics of a biomechanical system. For example, in drawing rhythmic circles, movement rate can be

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maintained by adopting the appropriate dynamics of an oscillatory system.

Although asserting the presence of two timing control processes may seem to lack parsimony, the distinction between event and emergent timing has been supported by a number of studies designed to test non-intuitive, neurophysiologically-based predictions. Most relevant for this paper is the work of Spencer et al. (16) showing that individuals with cerebellar pathology are selectively impaired on tasks theorized to require event timing. First, participants with unilateral cerebellar lesions were impaired in a timed tapping task, as well as an intermittent circle drawing task when each of these tasks were performed with the ipsilesional hand (the 'impaired' hand) compared to their contralesional hand (the 'unimpaired' hand). Of greater interest was the result that on the continuous circle drawing task, hypothesized to use emergent timing, performance of the ipsilesional and contralesional hands was virtually identical. In an additional experiment, only finger movements were performed, either produced intermittently (tapping or pausing prior to each cycle) or continuously. Again, an increase in variability associated with cerebellar pathology was restricted to the intermittent conditions, consistent with the predictions of the event timing hypothesis.

The initial work on the event/emergent dichotomy focused on the idea that distinct psychological representations and their associated neural systems underlie control of superficially similar tasks. One question that was ignored in this earlier work concerns the interaction between internal control processes and externally-defined task goals. In particular, how do participants establish the initial movement rate? For event timing, this is relatively straightforward: a target rate, indicated by a metronome, defines the target interval for the output of an internal timing system. This mapping process is consistent with claims that the cerebellum provides a common computation for perception and action. The metronome beats define salient temporal events and the cerebellum is important in the representation of these intervals, either for tracking the metronome, producing responses timed to be synchronized with these events (paced tapping), or for producing responses that mark similar events once the metronome is terminated (unpaced tapping).

But how is an externally defined temporal goal achieved when timing is emergent? People are generally quite good at producing rhythmic circles at a rate that closely matches a metronome-defined goal. Zelaznik et al. (1) proposed a transformation hypothesis in which the metronome guides an initial event-based representation. The participant adopts a movement rate based on previous experience and adjustments are instituted following a comparison of the produced and desired rate. Thus, timing during this initial phase is hypothesized to be event-based. The transformation to emergent timing for continuous movements occurs once the produced rate approximates the desired rate. At this point, the control system would no longer need to refer to an internal temporal signal. Rather, the dynamics could be sustained to keep the movement cycle constant at the metronome-defined rate. For example, in circle drawing, continuous variation of a spatiotemporal oscillator would suffice to maintain consistent timing by keeping angular velocity constant. Such a control scheme would not work for movements with discontinuities.

Zelaznik et al. (1) reported evidence in support of the transformation hypothesis. Using an individual difference approach with neurologically healthy individuals, they found that temporal variability was positively correlated between tapping and circle drawing on the first cycle of a repetitive movement. For subsequent intervals, the correlation was not significant. Thus, the initial cycle of circle drawing appears to rely on a timing process common to finger tapping. By the transformation hypothesis, this common process would be event-based timing.

Given our assumption that the cerebellum is critical for event timing, two predictions can be derived from the transformation hypothesis with respect to the performance of individuals with damage to this structure. First, if movement timing is initially event-based, then participants with cerebellar damage should show elevated temporal variability when drawing continuous circles on the first interval (or intervals). We test this prediction in the current experiment, calculating variability for each interval (interval 1 to interval 26) across trials. Note that this procedure is quite different than that adopted in most studies where variability is calculated within a trial (based on the values for each interval) and then averaged across trials.

Second, we speculate that the presence of a metronome signal may induce event-based timing, given that the tones define singular events for each cycle. While Spencer et al. (16) used a metronome in some of their experiments, these data were not analyzed. In the present study, participants performed trials in which the metronome was present for all 26 intervals (paced trials) or in which the metronome was only present for the first 7 intervals (partial-paced trials). If our speculation is correct, individuals with cerebellar damage should be impaired during the metronome-based intervals during both movement conditions. By including both paced and partial-paced trials, we are able to directly compare temporal variability at similar time points within a trial rather than confound paced and unpaced phases with the initial and latter phases of a trial.

Methods

Participants

Nine individuals with bilateral cerebellar degeneration (*ataxics*) were recruited for this study (Table I). For four of these participants, genetic testing confirmed a variant of spinocerebellar ataxia (SCA3: one participant; SCA6: three participants). A fifth participant has a familiar history of spinocerebellar ataxia (SCA3), indicating a likely diagnosis. For the remaining four participants, the etiology of their cerebellar degeneration was unknown. The ataxics were all evaluated with the International Cooperative Ataxia Rating Scale (ICARS, see (17)). The mean score (see Table I) was 40.7, with a range of 17.5 (mild to moderate) to 60 (severe).

MRI or CT scans were reviewed for all of the participants and confirmed that there was evidence of significant atrophy in the cerebellum. The extent and distribution varied considerably across the group. There was no evidence of significant atrophy in extra-cerebellar regions, although MRI and post-mortem studies of patients with certain SCA subtypes (e.g., SCA3) have reported pathology in the basal ganglia and brainstem (18,19). While some of our participants may have extra-cerebellar pathology, we expect that the pathology is most evident in the cerebellum, in accord with their clinical presentation.

A control group, on average matched in age and education to the ataxics, was also recruited. These individuals reported no history of neurological or psychiatric problems.

All participants provided informed consent, and were compensated for their time. The protocol was approved by the Committee for the Protection of Human Subjects at the University of California, Berkeley.

Task and procedure

Participants produced rhythmic finger tapping and continuous circle drawing movements. For finger tapping, movements involved flexion-extension of the index finger with the finger contacting a table surface at the end of the flexion phase. For continuous circle drawing, movements primarily involved rotation about the shoulder and elbow, similar to that employed in our previous studies (16). The participant held a cylindrical manipulandum (1 cm diameter, 3 cm tall) between the thumb, index and middle fingers, with the instructions to keep the tip of this object in contact with the table surface at all times. A 7 cm diameter circle was taped to the table surface to serve as a template for this condition. As in previous studies, the instructions emphasized that this template was to provide a guide for movement amplitude and that it was not necessary to carefully trace along the circumference.

The target cycle duration for all movements was 900 ms and a complete trial consisted of 26 movement cycles. The target interval was specified by an auditory metronome. This metronome was played at the start of each trial and the participant began to move when the rate was internalized (usually within 2 or 3 tones). We manipulated the number of cycles for which the metronome was presented following movement onset. In the paced condition, the metronome was present throughout the trial. In the partial-paced condition, the metronome was present

Table I. Population Data

Subject	Diagnosis	Gender	Age	Years since Diagnosis	Education	ICARS Total	Ataxia, Upper	Ataxia, Lower
P1	Atrophy	M	77	32	12	45	12.75	5.5
P2	SCA6	F	57	1	16	17	4	2
P3	Atrophy	M	68	15	17	42.75	13.5	8.5
P4	Atrophy	M	67	8	20	17.75	5	3
P5	SCA3	M	51	11	18	49.75	16.5	8.5
P6	Atrophy	M	54	10	14	34.5	4	2
P7	SCA6	M	52	6	16	21.5	5	0
P8	SCA6	F	46	12	16	54	16	4
P9	Atrophy/SCA3	M	72	8	12	60	18	3
C1	Healthy	F	75		19			
C2	Healthy	M	66		16			
C3	Healthy	F	65		18			
C4	Healthy	M	70		21			
C5	Healthy	F	61		16			
C6	Healthy	M	53		14			
C7	Healthy	M	52		12			
C8	Healthy	F	46		14			
C9	Healthy	M	72		12			
	Patient Average:		60.4, SD 10.7	9, SD 8.7	15.7, SD 2.6	40.7, SD 15.1		
	Control Average:		62.2, SD 10.0		15.8, SD 3.1			

until the participant produced seven movement cycles (seven circles or eight taps) and was then terminated for the remaining cycles. Thus, there were a total of four conditions, created by the factorial combination of movement type (tapping or circle drawing) and metronome status (paced or partial-paced).

The test session began with practice trials for two of the four conditions: finger tapping in the paced condition and continuous circle drawing in the partial-paced condition. Participants received practice trials until they understood both the required movements as well as the metronome conditions. Then each participant completed four blocks of trials (one per condition), with each block consisting of 10 trials. The order of the movement types (finger tapping, circle drawing) was counterbalanced across participants. Within a movement type, the two metronome variants were always tested in the order: paced then partial-paced. Participants were also tested with a third type of movement in which the circle drawing was performed in a constrained space (a grooved circular ring), with the idea that this apparatus might improve performance by reducing the demands on trajectory control. However, this device led to an increase in variability for all participants, perhaps due to the effects of friction or corrections generated when the hand contacting the edge of the groove. As such, we will not report these data.

Movements were recorded by a 3-dimensional kinematic tracking system (Ascension mini-Bird, http://www.ascension-tech.com). A magnetic transmitter was located below the table, and a lightweight sensor was secured with tape to the back of the index finger of the dominant hand, with the wire from the sensor secured loosely to the arm. The position of the sensor was sampled at a mean rate of 145 Hz. This sampling rate fluctuates slightly across trials, although not within trials.

Data analysis

Movement trajectories for each trial were analyzed using custom programs in MATLAB. First, the trajectories were smoothed using a 30-Hz Butterworth low-pass filter. For tapping, the duration of each cycle was then defined as the interval between successive contact points with the table surface. These contact points were identified with a velocity criterion, set as the first sample in which velocity fell below 3% of the maximum downward velocity for that flexion phase. For circle drawing, cycle duration was defined as the interval between successive crossings of the point on the circle most distant from the participant. In order to accommodate the impaired spatial trajectories of individuals with cerebellar degeneration, this point was identified on each cycle by a velocity criterion, and taken as the first point at which the velocity in the y-dimension fell below 3% of the maximum velocity along that axis. Using these criteria, the trajectories were marked into individual cycles using a semi-automated method with manual oversight (a procedure similar to that used in Zelaznik et al. (1)).

The data from each trial were divided into two phases, early and late. The early phase consisted of the first seven intervals. The metronome was present during these early intervals for both the paced and partial-paced conditions. Because preliminary analyses revealed no differences between the two conditions, we combine the early phase data across the two conditions to increase statistical power in the analyses. The late phase consisted of the remaining intervals (approximately 19 intervals). We report the late phase data separately for the paced condition (with metronome) and the partial-paced condition (without metronome).

For each trial, the mean and standard deviation of the cycle durations were calculated separately for the early and late phases. Note that for the paced condition, the division between early and late is arbitrary; for the partial-paced condition, this division corresponds to presence or absence of the metronome. To adjust for variation in the mean duration, the coefficient of variation (CV, standard deviation divided by the mean) was used as the measure of temporal variability. The CV was calculated independently for each trial and then averaged across the trials for a given condition. Intervals exceeding $\pm 50\%$ of the mean value for a given trial were excluded.

As a further test of the transformation hypothesis, we also calculated the mean and CV scores for each cycle defined by ordinal position (e.g., mean and CV for cycle 1, cycle 2, etc.; see ref (1)). For this calculation, the data are tabulated across trials rather than within a trial. Variability can be considerably inflated here if the overall rate varies significantly from trial to trial. In order to reduce effects caused by this form of trial-by-trial variation, cycle durations were normalized by dividing each interval by the mean cycle duration for that trial. The transformation test can be applied at two points in the partial-paced condition: at the start of the trial and when the metronome is turned off. As the trials for the paced and partial-paced conditions begin identically, we again combined the data across the paced and partial-paced conditions in the individual interval analysis of the early phase. This doubled the number of possible observations per participant for each interval (maximum of 20).

Results

Trials were excluded from analysis due to computer error (0.5% of trials for control participants, 1.3% of trials for ataxics) or the presence of extended pauses

between cycles (stopping for more than 50 ms during continuous circle drawing; 0.5% of trials for control participants, 3% of trials for ataxics). Of the remaining trials, individual cycles were excluded if the duration was greater than 150% or less than 50% of the mean cycle duration. This criterion caused the exclusion of 45 cycles for the ataxic group (approximately 0.5% of the total number of cycles; 6 during circle drawing, 39 during tapping) and two cycles for control participants (both tapping). After applying these various screening criteria, all trials had at least 22 cycles for the subsequent analyses.

Cycle duration

Figure 1 shows the mean cycle durations. Control participants generally produced mean cycle durations that were well-matched to the target rate of 900 ms. The mean produced duration for the controls is slightly faster than the target rate during the early phase of the trials. On some trials, the movements were initiated at a faster rate and subsequently slowed to the target rate over the first few cycles. The ataxics exhibited considerably more variation with some systematic deviations. During finger tapping, the ataxics moved more quickly than the target rate, both when the metronome was present ($t[16]=2.522$, $p=0.023$) and when it was absent ($t[16]=2.099$, $p=0.052$). However, when drawing circles, they moved considerably slower than the target rate (paced condition: $t[16]=3$, $p=0.008$; partial-paced condition: $t[16]=3.342$, $p=0.004$). It is possible that the target rate was faster than the ataxics were capable of producing; however, we do not expect that this provides a complete account of these data. In pilot work, we have observed a similar lack of correspondence between the target and produced rates even at slower and self-chosen rates.

Given that the early phase consisted of just seven cycles and there were strategic differences in how participants initiated the trials, our statistical analysis of cycle duration is restricted to the late phase. Note that the data from this phase come from the same

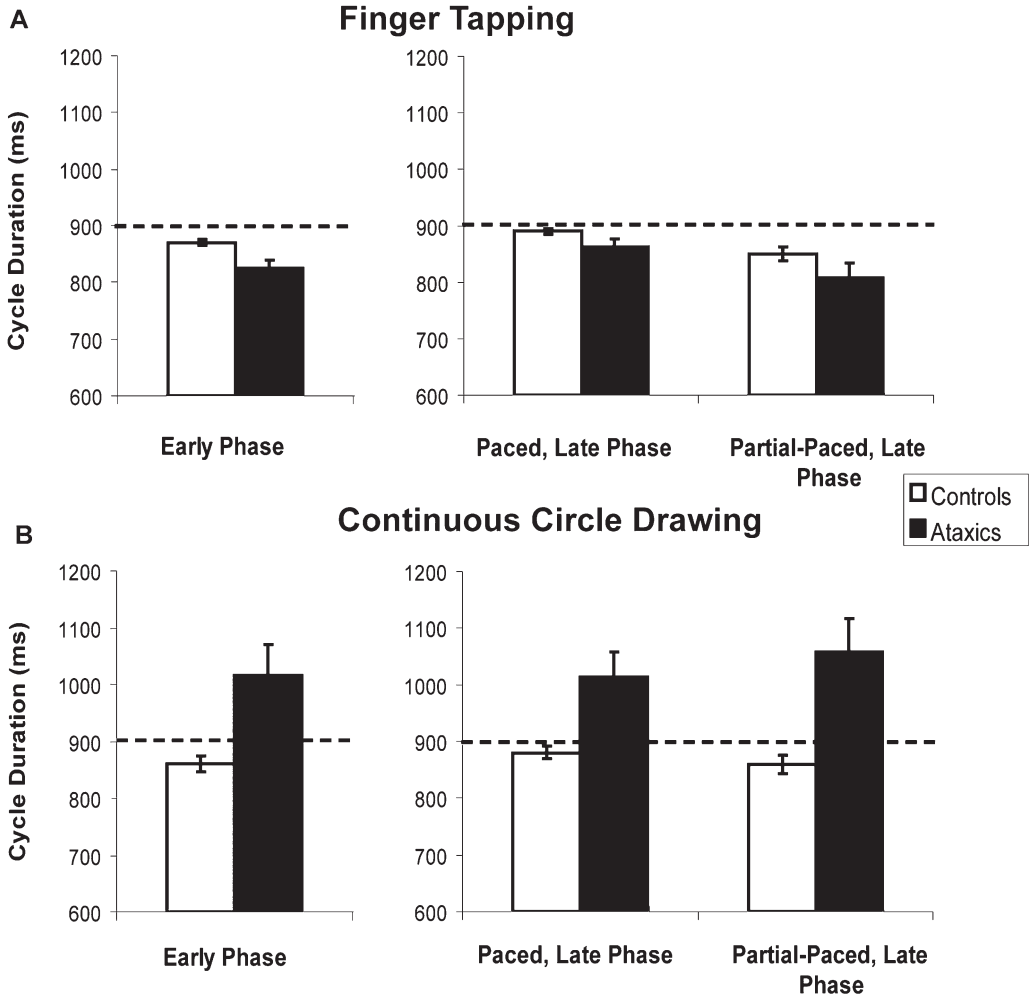

Figure 1. Cycle duration. Plotted are the average cycle durations, in milliseconds, across participants in the control group (white bars) or ataxic group (black bars). Error bars reflect standard errors. (A) Finger tapping. Ataxics are consistently faster than controls both during the early phase (first seven intervals) and the late phase (intervals 8 through 26) of both conditions. (B) Circle drawing. Ataxics are consistently slower than controls in all phases.

ordinal positions for the paced and partial-paced conditions. A $2 \times 2 \times 2$ ANOVA was conducted with within-subject factors of movement type (tapping vs. circle drawing) and metronome (present vs. absent) and the between-subject factor of group (control vs. ataxic). Significant main effects were observed for group ($F[1,16]=6.32$, $p=0.023$) and movement type ($F[1,16]=13.86$, $p=0.002$), while the effect of the metronome was marginally reliable ($F[1,16]=4.435$, $p=0.051$). Movement type interacted with group ($F[1,16]=13.89$, $p=0.002$) and metronome ($F[1,16]=13.65$, $p=0.002$) and the three-way interaction was also significant ($F[1,16]=6.03$, $p=0.023$). This interaction reflects the fact that the mean cycle duration for the patients was closer to the target rate when the metronome was present: during tapping this led to a slowing down of movement rate, and during circle drawing this led to a speeding up of movement rate. Thus, while the ataxics were not able to match their movement rate to the metronome as well as the control participants, their performance was influenced by the metronome. In the late phase of the trials, the mean cycle duration for the ataxics on both tasks was closer to the target rate when the metronome was present.

Event vs. emergent timing: Within-trial variability

Figure 2 presents the variability data calculated across cycles within a trial and then averaged over trials. We present two panels for each movement type: late phase of the paced condition, and late phase of the partial-paced condition. The late phase data allow a comparison of temporal variability over similar cycles (intervals 8–26) as a function of whether or not the metronome is present. To reduce the contribution of global drift in performance (e.g., speeding up or slowing down), the data were detrended by fitting a regression line to the data and measuring variability relative to the predicted value of this regression line.

The current design contains two of the key conditions reported in Spencer et al. (16) that provided neuropsychological evidence in support of the event/emergent distinction: unpaced rhythmic tapping and circle drawing following synchronization with a metronome. As can be seen in the figure, the results provide a partial replication. Consistent with Spencer et al., the ataxics exhibit a greater impairment than controls during finger tapping compared to circle drawing, in accord with the hypothesis that the former relies on event timing. However, unlike Spencer et al., the ataxics were also significantly more variable than controls during continuous circle drawing. The same pattern is found during the late phase of the paced conditions. Here, too, participants in the ataxic group were more variable than control participants and this difference

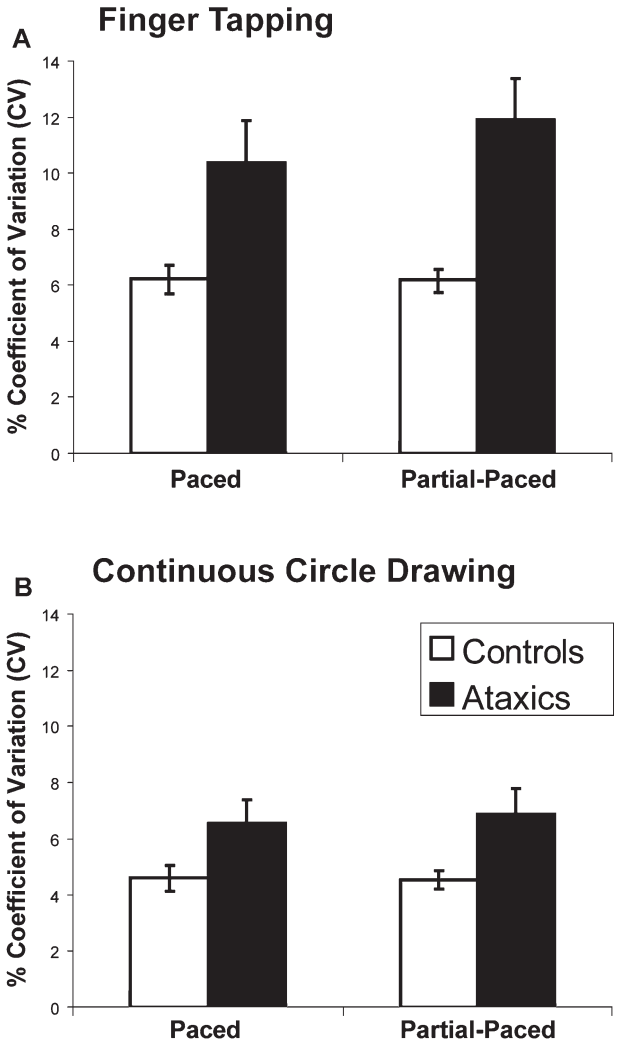

Figure 2. Trial variability during the late phase. Plotted are the average coefficients of variation (CV), calculated for each trial, for controls (white bars) and ataxics (black bars). Error bars reflect standard error. Ataxics are consistently more impaired during both finger tapping (A) and continuous circle drawing (B), though the impairment is more severe during finger tapping than circle drawing. The presence of the metronome during the paced condition lowered variability during finger tapping.

was larger (both in absolute percentage and proportionally) during tapping than circle drawing.

To statistically evaluate these effects, we performed the same 3-way ANOVA as for the cycle duration data, using the factors movement type, metronome, and group. The main effects of task (tapping vs. circle drawing) ($F[1,16]=65.0$, $p<0.001$) and group ($F[1,16]=10.6$, $p=0.005$) were reliable. More important, the interaction of these two factors was significant ($F[1,16]=11.9$, $p=0.003$); while the ataxics were more variable than the control participants on both tasks, their increase in temporal variability was significantly greater during tapping.

The controls were unaffected by the presence or absence of the metronome. In contrast, ataxics were less variable when the movements were paced by the metronome, resulting in a reliable group by

metronome interaction, ($F[1,16]=6.84$, $p=0.019$). Although the improvement during the paced portion appears to be restricted to tapping, the three-way interaction was not significant ($F[1,16]<1$). The fact that the performance of the ataxic group improved in the presence of the metronome is at odds with one prediction derived from the transformation hypothesis. If the metronome induced event-based timing, we expected the opposite pattern: a disproportionate increase in variability when drawing circles with a metronome.

Event vs. emergent timing: Between-trial variability

A stronger test of the predictions of the transformation hypothesis requires a microanalysis of the variability of individual intervals. As shown by Zelaznik and colleagues (1), only variability from the first interval during circle drawing was significantly correlated with tapping variability (on all intervals). These results were interpreted to indicate that an event-based temporal representation guides performance initially, allowing the performer to match the target interval of the metronome, before transitioning to control in which timing is emergent. Following this logic, we expected that individuals with cerebellar pathology would exhibit increased temporal variability when compared with control participants on the first interval in both tapping and circle drawing. The impairment during circle drawing should become attenuated over successive trials; in contrast, it should remain constant during tapping.

To assess this prediction, we calculated variability across trials on an interval-by-interval basis for the initial seven paced cycles (again, combining across the paced and partial-paced conditions to improve statistical power). Figure 3 shows these data for tapping (a) and circle drawing (b). For both conditions and for both groups, variability is highest on the first interval and then decreases to asymptotic levels by about the third interval. Contrary to the prediction of the transformation hypothesis, there is no indication that the ataxics were most impaired on the first interval during circle drawing. Indeed, in terms of mean values, the difference between the ataxic and control groups was actually smallest for this interval. When these data were statistically evaluated, a 2 (group) $\times$ 2 (movement type) $\times$ 7 (interval) ANOVA revealed a significant effect of interval ($F[1,16]=34.56$, $p<0.001$), but this factor did not interact with group, movement type, or the predicted 3-way interaction. Indeed, the only reliable interaction was between group and movement type ($F[1,16]=12.90$, $p=0.002$), reflecting once again that the ataxics were more variable during tapping.

Given that the CV was not equal during tapping and circle drawing (e.g., 19), we also compared the groups in terms of the percent increase in variability

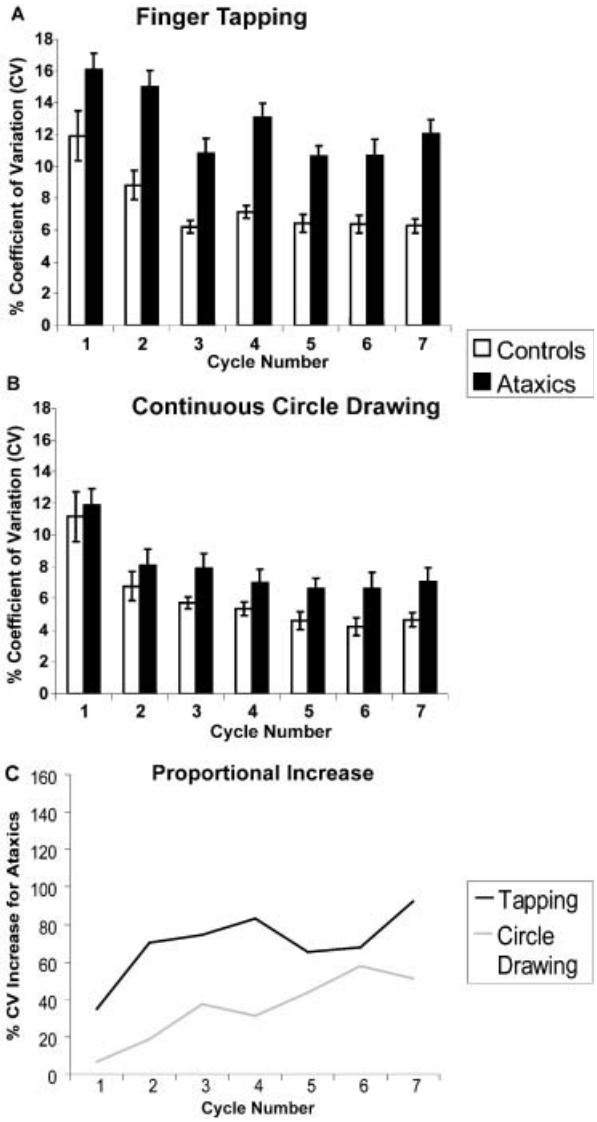

Figure 3. Interval variability during the early phase. CVs are calculated for each interval across trials following procedures detailed in the text. Paced and partial-paced conditions are combined, as the metronome is present for both conditions. Error bars reflect standard error of the mean. (A) Ataxics (black bars) are consistently impaired at all intervals during finger tapping. (B) Variability for circle drawing decreases for both groups after the first cycle, but ataxics remain impaired. (C) Plotted is the proportional impairment for the ataxic group relative to the control group. Unexpectedly, finger tapping (black lines) shows an increasing impairment over subsequent intervals. Contrary to the prediction of the transformation hypothesis, the proportional impairment on circle drawing (gray line) is lowest for the first interval.

on an interval-by-interval basis. On this measure, the transformation hypothesis would predict an interaction, where the ataxics become less impaired relative to controls over the course of a circle drawing trial. As can be seen in Figure 3c, the average divergence between the performance of ataxic and control participants actually increased over the course of these initial seven intervals. For circle drawing, the initial increase in variability was only 7%; by the seventh interval the increase was up to 51%. Thus,

the ataxics became proportionately more variable over successive intervals, opposite of the prediction of the transformation hypothesis. A similar trend was observed for tapping, with an initial 35% deficit rising to 92% by the seventh interval.

Finally, the transition from paced to unpaced movements in the partial-paced condition may offer another look at the transformation from event to emergent timing. Figure 4 plots the percent increase in CV for the ataxic group during the late phase, either with or without the metronome. We combined the data across pairs of cycles here since there are, at most, only 10 trials for each cycle. Again, there is no indication of a pronounced rise in variability during circle drawing when the metronome is turned off (Figure 4b). Rather, the timing deficit for these participants is relatively constant across the trial. The difference between the two types of movements was less pronounced in the late phase of the paced condition, in large part because the performance on tapping improved when the metronome was present.

Discussion

The cerebellar timing hypothesis was proposed as a system-level functional characterization of this subcortical structure. In its original formulation, the emphasis was on describing the functional domain of the cerebellum (e.g., 2). The ability to control the fine timing between successive gestures is a fundamental prerequisite for skilled movement. Similarly, precise timing is essential for certain forms of sensorimotor learning. While the timing hypothesis has offered a parsimonious account of cerebellar function over a range of task domains, there remains much to be understood about both the underlying mechanisms of internal timing and the specificity of

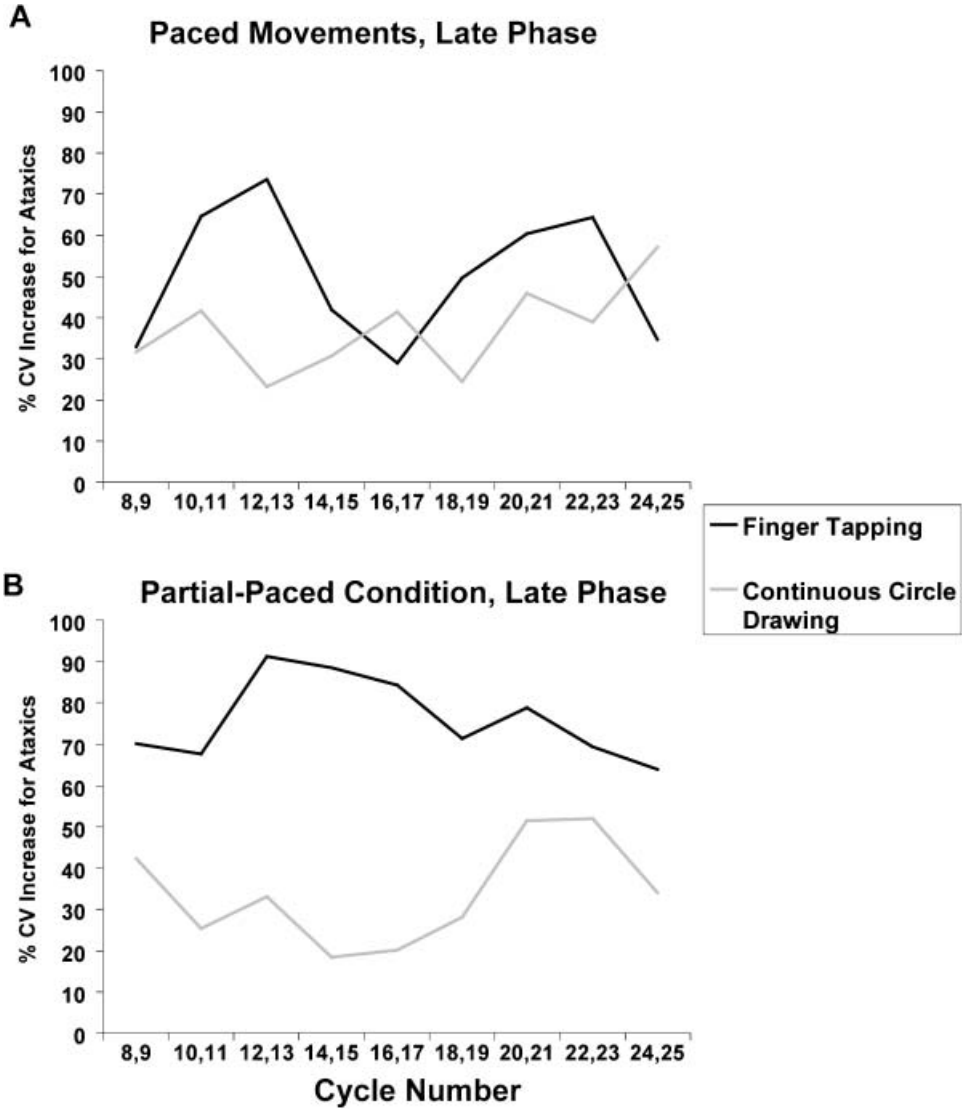

Figure 4. Interval variability during the late phase. Plotted are the proportional impairments for the ataxic group relative to the control group for intervals 8 through 25. To account for the slim data (10 trials per condition), CV was averaged across pairs of intervals. (A) During paced movements, ataxics are more impaired during finger tapping for most intervals, although there is some overlap in the curves. (B) During the partial-paced condition, in which the metronome is not present, patients are more impaired during finger tapping than during circle drawing at all intervals.

the cerebellum in timing. Indeed, the modular perspective explicitly motivating the timing hypothesis, that of a specialized system that is accessible to disparate neural systems requiring this form of representation, has been challenged by recent work suggesting that temporal coding may be a more local process (22–24). By this latter hypothesis, temporal representation may be a ubiquitous feature of neural processing, emergent in domain-specific representations. For example, the duration of a visual stimulus might be incorporated in the representation of the stimulus itself.

Event timing and the cerebellum

We have recently proposed a hybrid account of timing in which the functional domain of the cerebellum is limited to tasks in which an explicit representation of time is essential to the task goal. This event timing model was motivated by correlational work indicating that distinct processes were associated with the control of different classes of rhythmic movements (1,12–14). These findings suggested that, for movements marked by salient features, control might involve a process that encodes the requisite time between successive events. In contrast, when such features are absent, timing may be emergent, secondary to a more continuous form of control. Spencer et al. (16) reported that damage to the cerebellum selectively impaired performance on tasks linked to event timing, providing neuropsychological evidence for the role of the cerebellum in event timing.

Although secondary to the main purposes of the current study, we included tasks that were similar to those used in Spencer et al. (16). The results provide a partial replication. The participants with cerebellar degeneration exhibited a disproportionately greater impairment during finger tapping compared to circle drawing. The current results further extend our understanding by showing that this effect is not limited to movements performed in the absence of a metronome. Compared to controls, the relative impairment during finger tapping was evident both with and without a metronome.

Contrary to Spencer et al., the individuals with ataxia were also more variable than control participants during continuous circle drawing (see also, 25). This result seems especially puzzling given that many of the ataxic participants (6 of 9) in the current study had also participated in Spencer et al. (16). The disease process has advanced in some of these individuals and this may contribute to their greater variability in the current study. However, upon closer examination, the pattern of results is similar, despite the different statistical outcomes. In Spencer et al., the ataxic group showed a 13% increase in variability on the circle drawing task and a 56% increase during tapping compared to controls. This interaction was significant and a post-hoc contrast restricted to circle drawing was not reliable. In the current study, the percent increase in variability is 52% and 92% for circle drawing and tapping, respectively, with the interaction again significant as is the paired contrast for each task. Thus, the results from both studies emphasize a disproportionate impairment during tapping, consistent with the event timing hypothesis.

In Spencer et al. (16), the more dramatic dissociation of event and emergent timing was obtained in the within-subject comparison involving patients with unilateral lesions. The absence of any indication of a difference between the impaired and unimpaired limb during circle drawing led to the strong claim that the cerebellum was not involved in the control of continuous rhythmic movements. The current results suggest that this claim should be reconsidered. Alternative characterizations of cerebellar function, such as hypotheses suggesting putative roles for the cerebellum in forward modeling (e.g., 26–29), state estimation (e.g., 30,31), and error correction (e.g., 32), may suggest ways in which the cerebellum contributes to the control of both discrete and continuous rhythmic movements. However, it remains incumbent to explain why the cerebellum should be more heavily taxed during tapping compared to circle drawing. The emphasis on an essential role for the cerebellum in event timing offers one hypothesis (16,33).

The transition to emergent timing: Tests of the transformation hypothesis

We still do not understand how a rate is established in tasks which do not require the event timer. While consistent timing can be achieved during circle drawing by maintaining a constant angular velocity, the adopted velocity must produce cycles matched to the duration specified by a metronome. Zelaznik et al. (1) proposed that there is an initial transformation between event-based and emergent timing. Within the context of rhythmic movements, the initial movement cycle(s) may be compared to representations of an explicit temporal goal. Once an acceptable match is achieved, observably accurate timing could emerge from a secondary control parameter, at least in the absence of a metronome.

The primary goal of the current study was to test the transformation hypothesis, given the assumption that the cerebellum contributes specifically to event timing. As such, we expected that during circle drawing, the ataxics would exhibit increased variability during the early cycles of a trial compared to the latter cycles. We failed to obtain support for this prediction. The ataxic group did not show disproportionately elevated variability on the first interval; in fact, their impairment increased over successive cycles, similar to what was observed during tapping.

We do note that the best test of the transformation hypothesis comes from the first interval. However,

obtaining a reliable estimate of temporal variability for this interval is problematic. While we instructed the participants to begin moving when they had internalized the target duration, there are considerable fluctuations in how participants initiated their movements from trial to trial. Moreover, fluctuations in the internal representation of the target rate make it more difficult to obtain reliable estimates in a between-trial analysis compared to a within-trial analysis. In the latter, the mean of the central representation is assumed to be fixed for a given trial and noise about this mean reflects one source of temporal variability. Systematic changes within a trial (e.g., drift) can be discounted by simple analytic tools (e.g., linear detrending). These tools do not appear to be appropriate for a between-trials analysis, even though there are likely shifts in the mean between trials. Thus, it is more difficult to estimate between-trial variability because the observed intervals might reflect variation about a constant mean, shifts in that mean between trials, or some combination of the two. We attempted to correct for this by normalizing the mean duration on a trial-by-trial basis. Nonetheless, our data set is considerably smaller, and likely less reliable, than that used in Zelaznik et al. (1).

We also failed to obtain support for the transformation hypothesis in a second, within-trial analysis. If we assume that the metronome induces an event-based representation, then we expected that the ataxic group would become more variable when performing the circle drawing task with the metronome compared to when the metronome was absent. Contrary to this prediction, variability for the ataxics decreased when the metronome was present for both tapping and circle drawing.

It is interesting to note that control participants do not typically show a reduction in temporal variability during paced tapping compared to unpaced tapping. In fact, healthy individuals usually become more variable due to the operation of an error correction process (20,21,37), an effect that was present, although not reliably so, in the current study. Previous work has shown that error correction processes that operate during rhythmic movements are unaffected by cerebellar pathology (27,36). While a metronome leads to an increase in variability in healthy individuals, the observed improvement for the ataxic group during paced movements suggests that intact error correction and/or other processes influenced by the metronome may help offset increases in variability that arise from cerebellar pathology.

Conclusion

In summary, the predictions of the transformation hypothesis were not supported. At least two possibilities exist. First, the data set may not have been sufficiently robust to allow for a cycle-by-cycle analysis, the strongest test of the transformation hypothesis. Second, contrary to the assumption of Zelaznik et al. (1), the correlations observed between tapping and the initial cycle during circle drawing may not have reflected the use of an event-based representation in both tasks. Rather, the correlations may reflect the operation of a different, shared process that is especially relevant at movement onset. By this view, the current data indicate that the cerebellum is not involved with these initiation processes (33).

Note

1. In Zelaznik et al. (1), the initial cycle was produced in the absence of a metronome; in the current study, this interval was produced with a pacing metronome. We have conducted a study in which the metronome was terminated prior to the first movement cycle. Under those conditions, we also failed to observe a selective impairment on the initial cycles during circle drawing and between-trial variability was considerably larger (38).

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