The Cerebellum and Event Timing

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ABSTRACT: Damage to the cerebellum disrupts performance on a range of tasks that require precise timing including the production of skilled movements, eyeblink conditioning, and perceptual tasks such as duration discrimination. We hypothesize that such tasks involve event timing, a form of representation in which the temporal goals are explicitly represented. For example, during finger tapping, the goal to produce evenly paced intervals invokes an explicit temporal representation of the time between successive contact points with the tapping surface. In contrast, timing can be an emergent property in other actions, reflecting temporal consistencies that arise through the control of other movement parameters. One example is continuous circle drawing, a task in which temporal consistency can be achieved by maintaining a constant angular velocity or minimizing higher-order derivatives (e.g., jerk). Temporal consistency on event and emergent timing tasks is not correlated and patients with cerebellar damage show no increase in temporal variability during continuous circle drawing. While the cerebellum likely contributes to performance of a wide range of skilled behaviors, it appears to be especially important when the tasks entail event timing.

KEYWORDS: cerebellum; motor control; cognition; event timing; emergent timing

INTRODUCTION

We address two issues concerning the role of the cerebellum in motor control and, more generally, cognition. First, we review the hypothesis that the cerebellum can be characterized as an internal timing system. This hypothesis offers a functional account of how the cerebellum contributes to sensorimotor coordination, consistent with the clinical literature that has stressed the importance of this subcortical structure in the regulation of the temporal aspects of movement,[1,2] and suggests a general framework for how to conceptualize the operation of specific neural regions. Historically, behavioral neurology has tended to organize neural regions in terms of task domains. In this view, the cerebellum is considered part of the motor system, a prominent subcortical structure that can influence the output of both the extrapyramidal

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Ann. N.Y. Acad. Sci. 978: 302–317 (2002). © 2002 New York Academy of Sciences.

and pyramidal descending pathways. An alternative to this task-based division has its roots in the information processing approach that is central to cognitive psychology and, more recently, cognitive neuroscience. The emphasis of this approach has been to describe mental operations in terms of the representation and transformation of information. These computations are likely to be invoked across task domains, and recruited whenever their specialized operations are required.

Second, we turn to more recent studies from our laboratories that specify constraints on the functional domain of the cerebellum. Temporal regularities may be manifest in a wide range of behaviors. However, these regularities do not mandate an explicit representation of these temporal phenomena and, correspondingly, that timing is directly controlled. Indeed, we will argue for a fundamental distinction between tasks in which timing is explicitly represented and those in which timing is emergent. We review evidence consistent with this hypothesis and show that the cerebellum is especially critical for tasks that involve explicit temporal representations, situations that we describe as involving event timing.

CEREBELLAR TIMING IN MOVEMENT, LEARNING, AND PERCEPTION

The cerebellar timing hypothesis is intended to provide a broad characterization of the computational basis of cerebellar function. Precise timing is important for the production of skilled movements but is not the only computation required for skilled movement; thus damage to many other brain regions can disrupt skilled behavior. John Hore and colleagues (this volume), in a series of elegant studies of ball throwing, asked how the multiple actions across different joints can be efficiently and flexibly coordinated. Their results show that the timing of the opening of the fingers, required to release the gripped ball, is crucial for spatial accuracy. Moreover, this timing appears to be preprogrammed (i.e., open-loop), at least in skilled throwers. The lack of development of this temporal control can be seen in the poorly aimed throws of healthy individuals when using their non-dominant hand.[3] A breakdown in the temporal relationship between the forward movement of the limb and the ball release at the wrist is a cardinal feature of cerebellar damage.[4]

To provide a more direct test of the cerebellar timing hypothesis, we have generally opted to employ tasks that would, at least on the surface, appear to place a high demand on temporal control. Many of these studies use a repetitive tapping task in which the trial begins with the presentation of an auditory metronome indicating the target interval (FIG. 1A). Participants tap in synchrony with the tones for a short period of time and then are required to continue tapping when the tones end, trying to maintain the specified rate. Internal timing control is assessed by the overall variability of performance during this continuation phase, as well as by the application of a model that uses the covariance function of the time series data to provide estimates of two component sources of variability, one associated with motor implementation processes and a second associated with central processes including an internal clock (see Ref. 5). Patients with cerebellar lesions are impaired on this simple tapping task.[6] Interestingly, the increased implementation variability is associated with lesions of the medial cerebellum; in contrast, patients with lesions of the lateral cerebellar hemispheres exhibit a prominent increase in central variability.[7,8] This

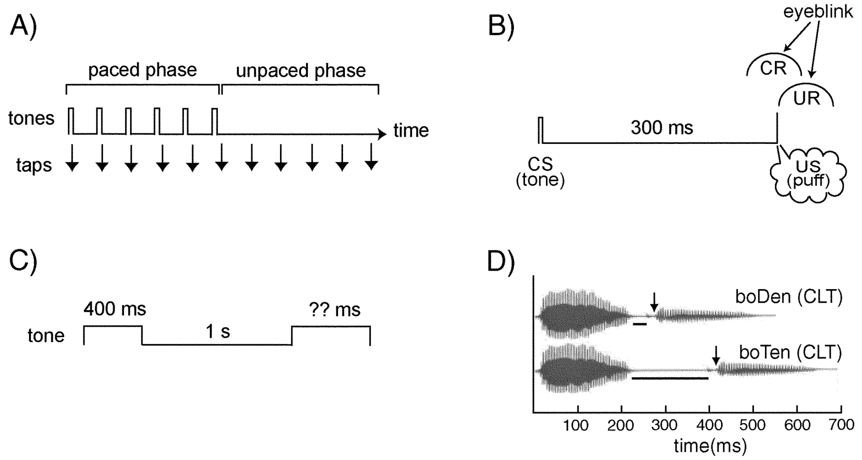

FIGURE 1. Schematic depiction of event structure in four tasks associated with timing functions of the cerebellum. (**A**) Repetitive tapping task. Participants are asked to produce series of evenly spaced responses. The primary dependent measure is the variability of intervals during unpaced phase. (**B**) Eyeblink conditioning. After repeated pairing of CS (conditioned stimulus) and US (unconditioned stimulus), animal learns to produce CR (conditioned respose) in anticipation of the US. (**C**) Duration discrimination. Participants judge whether comparison interval is shorter or longer than standard interval. A difference threshold is determined as measure of temporal acuity. (**D**) Speech perception. Perception of voiced or voiceless medial consonant is a function of duration of the silent interval between the two syllables [CLT (closure time)]. (Adapted from Ackermann *et al.*[17]).

dissociation is in accord with the anatomical projections of the cerebellum, given that the output of medial regions primarily targets descending motor pathways while the output from the hemispheric region influences the prefrontal, premotor, and motor cortex via thalamocortico projections.[9–11]

The timing functions of the cerebellum are not limited to motor control. A substantial literature has emerged over the past two decades implicating the cerebellum in simple forms of sensorimotor learning. For example, in eyeblink conditioning (FIG. 1B), an animal can learn to blink in anticipation of an aversive stimulus (e.g., an airpuff to the eyelid) following repeated pairings with a neutral stimulus (e.g., a tone). Such learning is only adaptive if the animal is able to learn the precise timing between the conditioned and unconditioned stimuli. Thus, the fundamental association is not only between two stimulus events, but also the precise temporal relationship of these events. Lesions of the cerebellum produce profound impairments on such forms of conditioning in a range of species, including rabbits, rats, turtles, and humans. While the exact locus of plasticity within the cerebellum remains contentious (see Yeo, this volume), the cerebellar cortex appears to play a critical role in regulating the fine timing of the conditioned response.[12] Detailed and highly constrained computational models of this task have been developed by a number of theorists (e.g., Refs. 13 and 14). Interestingly, these models have incorporated a range of mechanisms to allow for real-time representations, a feature that is typically absent in models of other neural learning systems.

Perceptual tasks that require precise timing also have been associated with the cerebellum (FIG. 1C and D). Patients with cerebellar lesions are impaired when asked to judge the duration of intervals in the range of 400 to 4 s.[6,15,16] These same patients do not exhibit comparable deficits when judging other properties of the same stimuli such as their intensity.

A more radical demonstration of the cerebellar role in temporal processing comes from the domain of speech perception. Most speech contrasts are signaled by a variety of cues. For example, the words "BOP" and "POP" can be distinguished on the basis of redundant cues: spectral differences exist in that the acoustic information is more dispersed at release for the /p/ sound. Temporal differences also exist in that energy at the fundamental frequency, generated by the periodic oscillations of the vocal cords, is delayed for the /p/. However, these sources of information can be isolated. For example, the temporal cues for "LABEL" and "LADLE" are essentially identical, with the distinction between the two sounds conveyed by the acoustic changes created by the way in which the airflow is occluded prior to the onset of the medial consonant. In contrast, words such as "BIDDEN" and "BITTEN" can be distinguished solely on the basis of a temporal cue, the period of silence at the time of occlusion. Patients with bilateral cerebellar degeneration are unable to discriminate between speech contrasts that involve purely temporal cues (FIG. 1D).[17] A recent functional imaging study has found that such sounds produce increased activation in only the cerebellum and inferior left frontal gyrus compared to speech perception conditions in which similar word contrasts required the analysis of spectral cues.[18] Perception of the latter sounds was associated with greater activation in the auditory regions of the superior temporal lobe. Thus, even a task as specialized as speech perception appears to engage a distributed network of processors. Presumably, these processors are invoked when their specialized computations, such as timing, are required.

While our emphasis has been on the timing functions of the cerebellum, it is important to note that other neural regions have been associated with the operation of an internal clock. These include the basal ganglia and regions of the frontal cortex, especially in the right hemisphere (reviewed in Ref. 19). It is possible that an amodal property such as time may be represented in a distributed or equipotential manner. For example, temporal codes may be derived from relatively slow physiological processes that operate across the brain.[20] At present, discrepant results in both the neuropsychological and neuroimaging literatures fail to provide a clear picture on this issue. At least some of the confusion here surely reflects the fact that even tasks as simple as repetitive tapping or duration perception involve many computations, and our analytic skills for isolating specific operations remain limited.

EVENT VS. EMERGENT TIMING

It is also possible that tasks may vary in terms of their requirements for a precise temporal representation or that the form in which temporal information is represented may vary as a function of task requirements. The Ackermann *et al.*[17] study emphasizes this point. The cerebellar patients performed normally in categorizing speech sounds that could be identified on the basis of either spectral or temporal cues. However, when only a temporal cue was available, their performance fell to near chance, reflecting the stringent demands placed on an internal timing system in this condition. Although there exist temporal regularities in the former condition, the patients were able to make the discriminations, presumably relying on computations involving the non-temporal cues.

Even when a task exhibits temporal regularities, it cannot be concluded a priori that these regularities will be represented in a direct manner. Consider the situation of waiting for your morning toast. Assuming that the heating element operates in a reliable manner, the amount of time required for the toast to reach the right level of brownness is relatively invariant from day to day. One could anticipate this moment by measuring the passage of time. Whether the cerebellar timing system is involved in such measurements is an open question; to date there have been few studies on the role of this structure in intervals spanning up to a minute. It is also possible that anticipating the opening of the toaster is not based on the ticking of an internal timer. From habit you might know that the toast will be ready just as soon as you take the butter out of the refrigerator and retrieve a plate and knife from the cupboard. Your behavior demonstrates a temporal consistency, yet there is no need to posit that a dedicated timing system is regulating all of these actions. Rather, the timing of these events is what we will call "emergent." Timing in this case may be highly subject to the vagaries of attention and arousal (e.g., Refs. 21 and 22). For example, if you are distracted by a particularly interesting story on the radio, you may be surprised to see the toast ready earlier than expected, perhaps inferring that the toaster was operating at a faster speed than normal.

Researchers of motor control have also stressed that temporal properties of movements can arise in an emergent manner, that is, without positing the explicit control of timing information.[23,24] For example, during bimanual circle drawing, temporal variability is much greater when the two hands follow parallel trajectories compared to when they follow mirror-symmetric trajectories.[25,26] This difference is not attributed to different control processes regulating the timing of the two types of movements. Rather, the increased timing variability is hypothesized to result from interactions created by the less compatible spatial requirements in the parallel condition. The temporal perturbations here, although regular and predictable, are emergent properties.

The idea that temporal properties differ across movement tasks is made clear in a series of studies reported by Zelaznik and colleagues.[27] Previous correlational studies had shown that the consistency of an internal timing system could account for a significant proportion of the variance between individuals in their performance on a range of motor and non-motor tasks.[28] Indeed, this correlational work had laid the groundwork for the studies of motor and perceptual timing in cerebellar patients. However, Zelaznik and colleagues failed to find such a dependency across a set of movement tasks. Across all of the tasks, participants were required to produce repetitive movements by tapping or drawing circles in different conditions. Each type of movement was performed at two different rates. A correlation matrix was constructed, using the normalized standard deviation as the primary indicator of temporal variability. Surprisingly, this matrix revealed that correlations were high across rates within a given task (e.g., tapping at 550 ms correlated with tapping at 800 ms), but were consistently low between tasks, even when rate was held constant (e.g., tapping and circle drawing failed to correlate when both were performed at 800 ms). Furthermore, correlations between tapping and circle drawing were low when both tasks were performed at the subjects' preferred rates.[29]

A number of differences exist between the movement tasks that might account for these null results. First, the movements involve very different sets of joints: while tapping involved flexion/extension of the index finger, circle drawing required movements about the shoulder and elbow. However, Keele *et al.*[28] had reported significant correlations between finger and foot tapping. Second, the spatial demands associated with the tasks were quite different. For example, tapping involves motion along a single axis and the only spatial requirement is that the finger touch the table in each cycle. In contrast, circle drawing requires that the participants maintain a particular spatial trajectory throughout the movement cycle. Third, the tasks appear

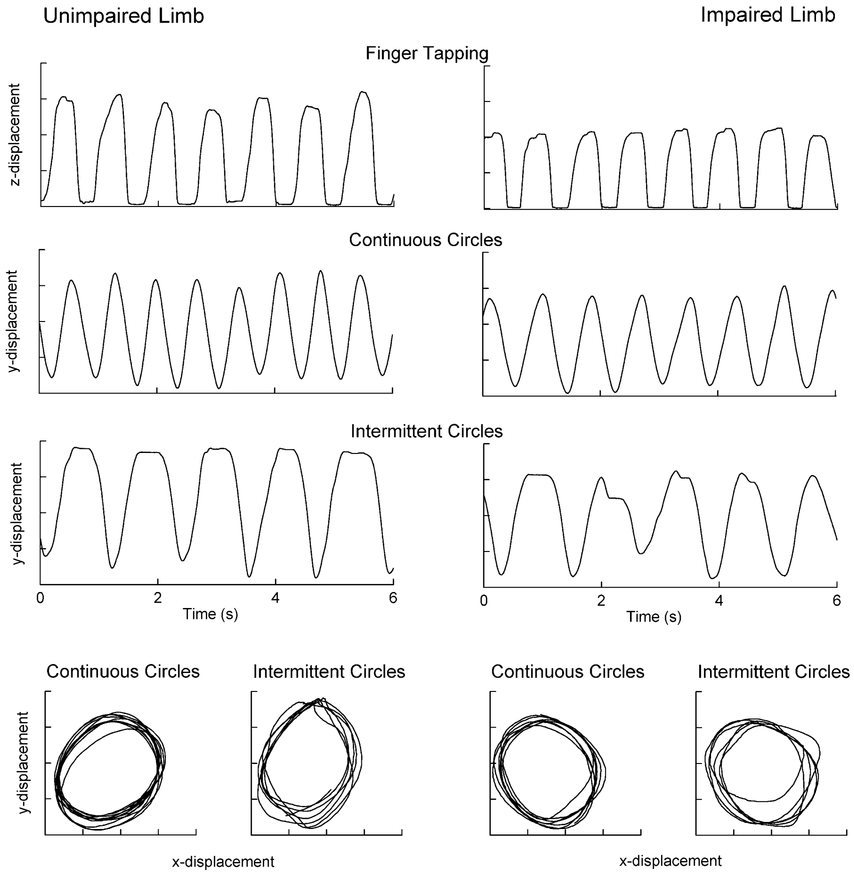

FIGURE 2. Kinematic traces from the performance of a patient with a unilateral cerebellar lesion on three repetitive movement tasks—finger tapping, continuous circle drawing, and intermittent circle drawing. Participants are instructed to insert a pause between each cycle in the intermittent drawing task. Note that a pause is introduced spontaneously during finger tapping at the point of maximum extension (*top of trace*). The pause at the point of maximum flexion indicates time during which the finger was in contact with the table surface. (Adapted from Spencer *et al.*[40])

to differ in terms of how they demarcate successive cycles. During finger tapping, each movement is separated from the next one by a small pause at the point of maximal extension. Thus, the series of movements have a discrete aspect to them, with certain points such as the onset of each downstroke or the contact with the table being especially salient (FIG. 2). The drawing tasks used by Robertson *et al.*[27] are of a more continuous nature. Perhaps such differences are also reflected in the control operations. For example, models of tapping have embodied discrete notions such as singular points at which central timing commands are directed to the periphery, with much of the operation being open-loop.[30–33] In contrast, models designed to account for temporal regularities during the drawing of curved shapes have focused on more continuous variables such as angular velocity (e.g., Refs. 34 and 35).

We designed a study to compare these hypotheses.[37] Two of the tasks had been included in the earlier studies, finger tapping and continuous circle drawing. The third task, intermittent circle drawing was designed to be a hybrid. For this task, the participants were instructed to divide each cycle into two parts, a movement phase in which they were to produce a complete circle, and a pause phase in which they were to remain at one position. The pitch of the pacing signal alternated, and the participants were instructed to begin each movement phase with the high-pitched tone and end this phase with the onset of the low-pitched tone, thus attempting to alternate between a 400-ms movement and a 400-ms pause. Spatial and temporal measures were obtained for all three tasks, with the focus of our analysis on the variability of cycle duration.

The intermittent and continuous circle drawing tasks involve similar joint movements and spatial demands. If either of these factors were critical in terms of the underlying sources of temporal variability, we should observe a high interindividual correlation between these two tasks, and performance on neither task would correlate with tapping. On the other hand, if the key variable centers on whether the tasks are conceptualized as composed of continuous movements or a series of discrete events (e.g., tap or circle onset), then performance on the tapping and intermittent circle drawing tasks would be correlated. The results clearly favored the latter hypothesis. The correlation between the tapping and intermittent circle tasks was .50. In comparison, the correlations between the continuous circle task and the other two tasks were below .30. Performance on the two circling tasks did correlate with one another on a measure of spatial consistency. Nonetheless, the surprising result was that on the measure of temporal variability, these two circle drawing tasks were only weakly related whereas a strong correlation was found between temporal variability on tapping and intermittent circle drawing.

In the experiment described above, the target cycle duration for all three tasks had been 800 ms. Given that the movement phase of the intermittent circling task was completed in approximately half of this time, the movements were performed at a considerably higher velocity than in the continuous circling task. A second experiment was conducted to roughly equate movement velocity across these tasks.[37] The cycle duration was reduced to 400 ms in the continuous circling condition. It remained at 800 ms in the intermittent condition. In addition, we included a perception task, duration discrimination, to measure non-motor temporal acuity.

The results closely replicated that of the first experiment. Significant correlations were again observed between measures of temporal variability on the tapping and intermittent circle drawing tasks. Neither task correlated with temporal variability on the continuous circling task. Even more impressive, both temporal consistency during tapping and intermittent circling were correlated with temporal acuity on the perception task (values of .39 and .56, respectively). The correlation between the perception task and continuous circle drawing was −.15.

In sum, the results clearly point to a shared timing process involved in finger tapping, multijoint intermittent circle drawing, and time perception. While the positive correlations between these three tasks are impressive, it is equally important to note that this shared process is not generic. Temporal variability on the continuous circle drawing task was not related to these three tasks. We hypothesize that an explicit representation of temporal information is the commonality between the tapping, intermittent circle drawing, and duration discrimination tasks. We refer to this as event timing, to capture the idea that the actions or judgments are made with reference to this explicit temporal representation. In tapping, the representation may be of the desired time between successive downstrokes or taps.[38] Similarly, for participants to consistently maintain a target cycle duration in the intermittent drawing task, they must account for both the movement and pause time. As such, an efficient representation of the task goal would be to include an explicit representation of the time between the onsets of successive cycles. We also posit that judging the duration of an empty interval requires that the interval be explicitly represented and compared with a representation of an internalized standard interval.

In contrast to tasks that entail event timing, we suggest that temporal regularities can also occur without explicit temporal representations. We refer to these temporal properties as emergent or secondary to some other form of control. At present, we can only speculate as to what this type of control might be. For continuous circle drawing, one hypothesis would build on the idea that optimal performance occurs when angular velocity is held constant.[35] A related idea would be that control here would be based on operations that minimize discontinuities in the velocity profile (or higher-order derivatives such as jerk; see Ref. 39). This is not to ignore the fact that the participants are easily able to produce the circles to match the target duration defined by the metronome. We propose that at the beginning of each trial an explicit temporal representation is derived based on the intervals constructed by the beats of the metronome. However, this representation is then transformed into some other control parameter that allows the circles to be completed within the target duration. In this manner, timing during continuous circle drawing is emergent in that the goal is represented in terms of a target velocity or some other secondary form of control rather than explicitly defined temporal events. This form of control would, of course, fail to work for intermittent circling because, by definition, the task requires periods of zero velocity. In a similar manner, the salient points within the tapping cycle appear to favor an event-based representation rather than a representation that reflects some sort of continuous control signal.

EVENT TIMING AND THE CEREBELLUM

The correlational studies reviewed above provide compelling behavioral evidence that non-identical control processes are involved in the timing of repetitive movements that are either performed in a continuous or segmented manner. We have also investigated this dissociation in a series of neuropsychological studies.[40] In our

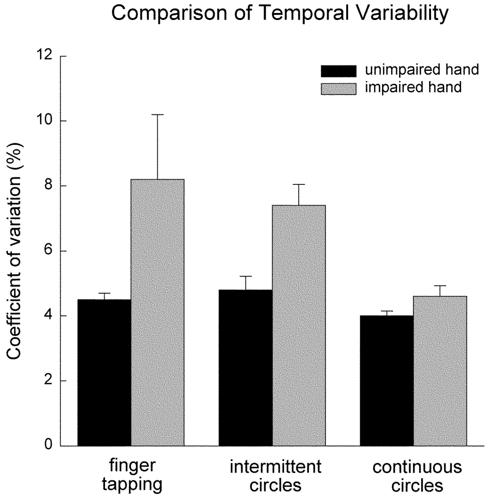

FIGURE 3. Temporal variability on the three movement tasks for a group of patients with unilateral cerebellar lesions. To compensate for differences in movement rate, the results are expressed in terms of the coefficient of variation (standard deviation of the intervals divided by the mean interval). (Adapted from Spencer *et al.*[40])

first study, patients with focal lesions of the cerebellum were tested on three tasks: finger tapping, continuous circle drawing, and intermittent circle drawing. The target cycle duration was fixed at 800 ms with the instructions in the intermittent circling task emphasizing that this interval should be divided into a movement phase and a pause phase. The patients performed each task twice, once with the ipsilesional, impaired limb and once with the contralesional, normal limb. In this manner, each person served as his or her own control. The patients were tested at least one year after their stroke or tumor resection surgery, at a point where their cerebellar symptoms were stable. In fact, some of the patients showed minimal sign of cerebellar dysfunction at the time of testing.

As our primary dependent variable, we used a normalized measure of temporal variability, dividing the standard deviation of the cycle durations by the mean cycle duration. Given that timing variability increases with cycle duration,[32,41] this measure allowed us to compare variability scores across tasks and hands even if the actual produced cycle durations were unequal. Replicating earlier findings,[7,8] the patients were more variable when tapping with their ipsilesional hand. A similar deficit was also observed on the intermittent circle drawing task. However, no difference was found on the continuous circle drawing task (FIG. 3).

We introduced two changes in a second experiment to further explore this dissociation. First, in addition to the patients with unilateral cerebellar lesions, we also tested patients with bilateral cerebellar degeneration and age-matched control participants. Second, the tapping and intermittent circling tasks were modified such that the intervals within a trial were produced one at a time with a random interval separating successive productions rather than as a continuous series. During the pacing phase, two sounds were presented, defining the target interval for either two taps or one circling cycle. During the continuation phase, a single tone indicated when the participants should produce the next response, trying to match the target duration for a single cycle. The results replicated what had been observed in the first experiment. The unilateral patients were selectively impaired on the single cycle circling and tapping tasks when using their ipsilesional limb. Similarly, the bilateral patients were more variable than the controls on these two tasks. Importantly, both patient groups performed comparable to the controls on the continuous circling drawing task.

The lack of a deficit on the continuous circle drawing task is quite striking. While the correlational work had suggested that this task involved different control processes, a priori, it seemed reasonable to expect that cerebellar dysfunction would also be manifest during circle drawing with the ipsilesional arm. Indeed, there were a number of reasons to expect that this task would place greater demands on the cerebellum than finger tapping. First, the average movement speed is much greater during circle drawing given that the circumference of the circle is about five times greater than the amplitude of tapping. Second, the circle drawing condition required more visuomotor control given the participants were provided with a visual template for this task. Third, circle drawing requires coordination across the shoulder and elbow joints. Such multijoint movements will generate interactional torques that are likely minimal during finger tapping. All of these variables—movement speed, visuomotor control, multijoint coordination, and interactional torques—have been shown to be sensitive to cerebellar dysfunction.[42] Yet the results show that the patients exhibited no impairment when the circles were produced in a continuous manner.

We believe that the distinction between event and emergent timing provides the most parsimonious account of these results. In this view, the cerebellum is essential for those tasks that involve event timing. It provides the explicit representations that specify the timing of these events: when the next tap should be produced or when the next movement cycle should begin during intermittent circle drawing. The null findings with respect to the continuous circling task suggest that the cerebellum is not a critical component of the control processes for tasks in which timing is emergent. At present, we have little to say about the neural mechanisms that control timing during continuous circle drawing. As proposed above, optimal performance here can be achieved by maintaining a constant angular velocity. From this, we would infer that the cerebellum plays, at most, a secondary role in the control of the relevant parameters for these continuous movements. We suspect that cortical mechanisms might be primary. However, it remains to be seen whether the reverse pattern of results would be obtained in studies with a different patient group: namely, a selective impairment on the continuous circle drawing task.

TEMPORAL COORDINATION DURING CONTINUOUS AND DISCRETE MOVEMENTS

The performance of callosotomy patients during bimanual movements provides converging evidence of a dissociation between subcortical and cortical systems in the temporal coordination of tasks that involve discrete movements and those that involve continuous movements. A number of studies have shown that the two limbs remain temporally coupled during such movements.[43–45] However, we recently tested three callosotomy patients on a version of the continuous circle drawing task, under conditions in which the participants were asked to move at their preferred speed or at maximal speed.[46] A second variable was based on the direction of the two hands. The hands either followed symmetric trajectories (e.g., one clockwise rotation, the other counterclockwise) or asymmetric trajectories (e.g., both clockwise). Control participants have been shown to exhibit less temporal stability, expressed as an increase in variability of cycling time and relative phase between the hands when the hands perform asymmetric movements, especially when performing at maximal speed.[26] This instability has been modeled as resulting from the interactions of coupled spatiotemporal oscillators. We found that the callosotomy patients did not show this difference between symmetric and asymmetric circling. More importantly, the patients exhibited a striking lack of temporal coupling during all circling conditions. Indeed, the two hands frequently moved at completely different frequencies. This suggests that in normal individuals the interaction between the two hands during continuous circle drawing involves intercortical processing mediated by callosal fibers.

The previous reports of persistent temporal coupling in callosotomy patients had all involved movements containing a discrete event, such as the contact with an object[44,45,47] or the on- and offset of movements while drawing line segments.[43] To directly test whether the inclusion of such discrete events is critical, we tested the patients on two modified “tapping” tasks.[46] In both, the movements were restricted to flexion and extension of the index fingers, and these movements were made in the air (e.g., no tactile feedback from contacting a surface). In one condition, the participants were instructed to make the movements continuously, with smooth transitions between flexion and extension. In the other condition, they were instructed to insert a pause prior to each flexion onset. This subtle manipulation produced a dramatic change in performance. Whereas the degree of temporal coupling was similar for control participants under both conditions, the callosotomy patients exhibited a threefold increase in the standard deviation of the phase differences in the continuous movement condition. Similar to what we had observed in circle drawing, the two hands exhibited extended epochs of temporal uncoupling (FIG. 4).

When considered in combination with the studies of cerebellar patients, a consistent story begins to emerge. The temporal control of continuous, rhythmic movements does not invoke the cerebellar timing system. The temporal regularities observed under such conditions are emergent; there is no explicit representation of timing signals once the initial temporal goal has been transformed into a different control parameter. Our working hypothesis is that the control of such movements is cortically mediated, perhaps through the operation of an oscillatory process that regulates smooth changes in spatial variables over time. During bimanual movements, these oscillators become coupled. We assume that these interactions involve cortically based representations and that interhemispheric communication is primarily dependent on the corpus callosum. Such a mechanism can also account for spatial compatibility effects that are observed during bimanual movements.[48]

In contrast, the temporal control of a repetitive series of discrete movements requires an explicit temporal representation. Psychologically, this representation specifies when particular events should occur or have occurred. Timing remains an explicit part of the representation of the task goal. We hypothesize that the cerebellum is specialized for providing this explicit form of temporal representation. In finger tapping, the cerebellum signals when the next response should occur. In other

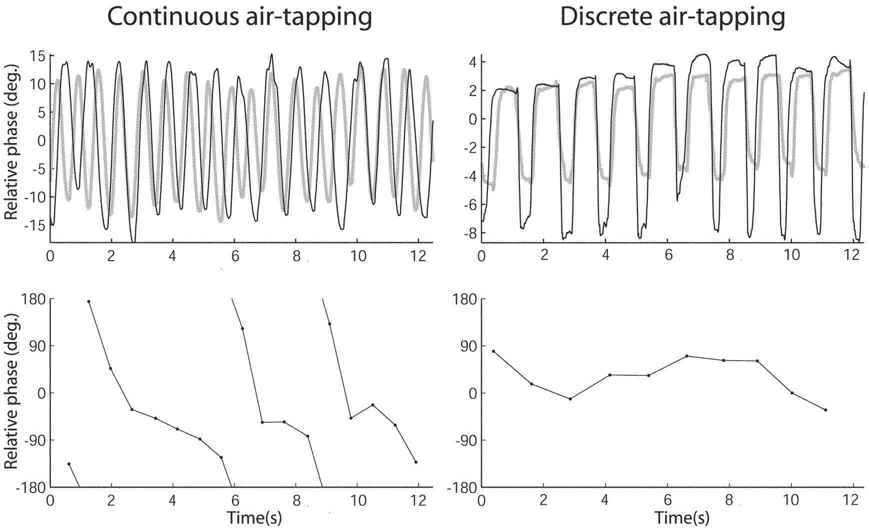

FIGURE 4. Kinematic traces produced by a callosotomy patient during two bimanual finger movement tasks. In the discrete task, the instructions emphasize that a brief pause should be made prior to each flexion phase. In the continuous task, the instructions emphasize that the movements should be made as smoothly as possible. The patient's movements are temporally uncoupled in the continuous condition but remain coupled in the discrete condition. (Adapted from Kennerley *et al.* [46])

work, we have proposed that independent temporal control signals for each finger are generated within the cerebellum during bimanual tapping, but that these signals are constrained to act through a common, subcortical gate. This gating process introduces a nonlinearity in the control process, retaining the event structure of the representation of these movements.[31]

SUMMARY

Our previous work has emphasized the contribution of the cerebellum in tasks that require a precise representation of temporal information. The cerebellar event-timing hypothesis specifies an important boundary condition for this functional account of the cerebellum, underscoring the observation that while temporal regularities may be observed in a wide range of behaviors, the use of an explicit representation of temporal information may be more limited.[49] In our work to date, we have compared two classes of repetitive movements, those which are performed in a continuous manner and those in which the successive actions are marked by some discrete event or boundary such as a finger tap or pause. We also believe the notion of event structure applies to other temporal processing tasks that have been linked to the cerebellum. For example, eyeblink conditioning requires the association of two salient events and the interval that separates them. Similarly, speech perception tasks that are dependent on the cerebellum are ones in which the only cue is the duration of a silent interval that separates two articulatory events.[17]

An obvious question is, how does one specify tasks that entail an event structure? The hypothesis would risk becoming circular if the defining criterion were based solely on determining whether or not the task presents difficulties for patients with cerebellar lesions. One way to address this concern is by looking for converging evidence such as in our studies with callosotomy patients, or with other methodologies. Computationally, one can ask whether the underlying representations embody the notion of an event structure. For example, Semjen and Ivry[50] have argued that limitations in bimanual tapping should be attributed to the manner in which the temporal goals are represented rather than to the dynamics of coupled oscillators. In support of this view, they observed that identical rhythmic distortions are found for uni- and bimanual tapping, reflecting a common event-based representation.

The event timing hypothesis is also likely to be relevant in evaluating the current debate about the relationship of timing and prediction. Representing when the next tap should occur or when an airpuff will be experienced are, of course, forms of prediction. It has been proposed that the fundamental property of cerebellar function is its operation as a predictive device. In sensorimotor control, this idea is captured by the formalism of internal, forward models.[51,52] More generally, this idea has been offered to account for putative cerebellar contributions to higher-level cognition such as language, problem solving, and attention.[53,54] For example, the cerebellum might contribute to problem solving by supporting internal simulations that test out possible solutions to see if the end result matches the goal. While the empirical evaluation of such ideas is limited at present, the event timing hypothesis offers a conservative starting point for assessing the role of the cerebellum in cognition. Prediction is ubiquitous. However, there is a difference between anticipating something in a generic sense and specifying when that event will occur.[55] We expect that, similar to motor control, the functional domain of the cerebellum in cognition will be limited to situations that require real-time predictions.

ACKNOWLEDGMENTS

This work was supported by NIH grants NS 30256, NS 1778, and DC 02527, and the National Science Foundation grant ECS-9873474.

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