Comparison of patients with Parkinson's disease or cerebellar lesions in the production of periodic movements involving event-based or emergent timing

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Abstract

We have hypothesized a distinction between the processes required to control the timing of different classes of periodic movements. In one class, salient events mark successive cycles. For these movements, we hypothesize that the temporal goal is a requisite component of the task representation, what we refer to as event-based timing. In the other class, the successive cycles are produced continuously. For these movements, alternative control strategies can optimize performance, allowing timing to be emergent. In a previous study, patients with cerebellar lesions were found to be selectively impaired on event-based timing tasks; they were unimpaired on a continuously produced task. In the present study, patients with Parkinson's disease were tested on repetitive movement tasks in which timing was either event-based or emergent. Temporal variability on either type of task did not differ between on- and off-medication sessions for the Parkinson's patients nor did patient performance differ from that of controls. These results suggest that the basal ganglia play a minimal role in movement timing and that impairments on event-based timing tasks are specific to cerebellar damage.
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1. Introduction

On a daily basis, we are capable of tracking time; we can do this explicitly by watching a clock or we can track time less directly. For instance, you could be aware that it is 9 a.m. by referencing the clock on the wall, or because you have brushed your teeth, showered, walked the dog, and biked to work. On a more minute time scale we are also capable of tracking time. While driving, you must release the clutch at a precise time relative to stepping on the gas. Likewise, for accuracy when throwing a ball, you must open the fist at a precise time within the swing of the arm (Timmann, Watts, & Hore, 2000).

Recent studies have revealed that timing in the millisecond range can also be explicit or indirect. In the former case, timing occurs through the operation of an internal clock-like process in which the temporal goal is explicitly represented. By explicit, we do not mean conscious; to avoid confusion with the manner in which this term is used in studies of memory, we will refer to this process as event-based timing. For other tasks, timing is indirect; in these tasks timing is hypothesized to be emergent, resulting from the operation of non-temporal parameters such as muscle stiffness.

The distinction between event-based and emergent timing was motivated by a series of studies by Zelaznik and colleagues (Robertson et al., 1999; Zelaznik, Spencer, & Doffin, 2000). They compared the performance of healthy young adults on two tasks that have been

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widely used to study motor timing, finger tapping and continuous circle drawing. Previous correlation studies had suggested a common timing process was engaged across a range of rhythmic, motor tasks (Franz, Zelaznik, & Smith, 1992; Keele & Hawkins, 1982; Keele, Pokorny, Corcos, & Ivry, 1985). Based on these results, significant correlations were expected between temporal variability on the continuous circle drawing task and the tapping task. However, timing variability of these two types of movements did not correlate.

A key distinction between the continuous drawing task and the finger tapping task is that optimal performance on the circle drawing task requires the movements to be made in a smooth, continuous manner. In contrast, finger tapping is best viewed as the concatenation of a series of distinct cycles: Not only does the tapping surface define each cycle, but people tend to impose a slight pause prior to each downstroke. To assess the importance of the continuous/discontinuous distinction, Zelaznik, Spencer, and Ivry (2002) introduced a hybrid circle drawing task. In this task, subjects were instructed to pause between each circling cycle. In spite of the similarity between this task and continuous circle drawing, temporal variability on the intermittent circle drawing task correlated with tapping and neither task correlated with continuous circle drawing. We hypothesized that for the discontinuous movements an explicit event-based representation of the temporal goal is required, specifying the timing of critical events such as the onset of each cycle. In contrast, for continuous movements, timing is emergent. People are, of course, able to match the rate of continuous movements to an externally-defined temporal goal (i.e., movement rate), but this can be achieved by varying a non-temporal control parameter such as joint stiffness (see Ivry, Spencer, Zelaznik, & Diedrichsen, 2003).

These individual difference studies pointed towards a distinction between tasks in which timing was either event-based or emergent. Further support was obtained in a series of studies involving patients with acquired cerebellar lesions. The patients exhibited increased temporal variability on the finger tapping and intermittent circle drawing tasks. However, they performed comparable to control participants on the continuous circle drawing task (Spencer, Zelaznik, Diedrichsen, & Ivry, 2003). The deficits on the event-based timing tasks are consistent with neuropsychological (e.g., Ackermann et al., 2001; Ivry, Keele, & Deiner, 1988) and neuroimaging studies (e.g., Jueptner et al., 1995; Kawashima et al., 2000; Penhune, Zatorre, & Evans, 1998) indicating that the cerebellum is essential for the precise representation of temporal information. The lack of an impairment on the continuous circle drawing task, despite the added complexity of this task in comparison to tapping, suggests that the cerebellum is not essential for tasks in which timing is emergent.

The basal ganglia have also been associated with temporal processing. Manipulation of dopamine levels in rats and humans has been shown to alter the rate of perceived time, an effect attributed to the slowing or speeding of an internal clock (e.g., Meck, 1983, 1996, 2003; Meck & Benson, 2002). Neuroimaging studies have also associated basal ganglia activity during timing tasks with temporal processing requirements (Coull, Vidal, Nazarian, & Macar, 2004; Harrington, Haaland, & Hermanowitz, 1998a; Hinton & Meck, 2004; Nenadic et al., 2003; Rao et al., 1997). The results from patient studies have been less consistent. While some studies have reported that patients with Parkinson's disease (PD) exhibit similar deficits as those observed in patients with cerebellar lesions (CE) (Harrington, Haaland, & Knight, 1998b; O'Boyle, Freeman, & Cody, 1996; Pastor, Jahanshahi, Artieda, & Obeso, 1992), other studies have found that the PD patients perform similar to neurologically healthy controls (Duchek, Balota, & Ferraro, 1994; Ivry & Keele, 1989).

In the current study, we tested PD patients on the tapping, intermittent circle drawing, and continuous circle drawing tasks. The study provides another assessment of the performance of PD patients on motor timing tests, adding to the empirical base for what has turned out to be a problematic issue. Of greatest interest, the study provides a test of whether the event-based/emergent timing distinction can be dissociated neuropsychologically. It may be that deficits on the tapping and intermittent circle drawing tasks are observed in various patient groups with motor impairments. That is, these two tasks may be more sensitive to the effects of neuropathology than the continuous drawing task. On the other hand, finding that the PD patients were unimpaired on the tapping and intermittent drawing tasks would provide new support for the hypothesis that the cerebellum is specialized for event-based timing. Two other results are possible. First, the PD patients might be selectively impaired on the continuous circle drawing task, a result that would constitute a double dissociation when combined with the CE patient findings. Second, PD patients may be impaired on all three tasks.

2. Method

2.1. Participants

Eight patients with a diagnosis of idiopathic Parkinson's disease and eight age- and education-matched controls volunteered in exchange for payment.

Patient volunteers were given a neurological exam to assess motor function as well as a series of neuropsychological tests to evaluate cognitive status. Those exhibiting signs of dementia or marked cognitive impairment were excluded. Neuropsychological and demographic

Table 1
Descriptive variables across tasks

	PD patients				Controls	
	On-meds		Off-meds		D	ND
	D	ND	D	ND		
Finger Tapping	557.7	557.9	542.4	541.4	533.8	537.5
	(22.9)	(20.2)	(11.6)	(14.0)	(15.7)	(10.3)
Intermittent Circles						
Total	1066.2	1114.1	1072.4	1214.8	1065.8	1144.0
	(48.2)	(58.7)	(37.3)	(95.0)	(37.7)	(41.9)
Movement	777.0	793.6	829.4	963.2	733.0	843.6
	(30.2)	(33.8)	(42.2)	(77.7)	(29.3)	(32.3)
Pause	287.5	313.1	236.9	254.4	343.8	288.9
	(33.0)	(39.2)	(38.1)	(35.2)	(29.0)	(36.7)
Continuous Circles	540.5	593.7	546.1	702.1	543.1	627.0
	(21.4)	(19.9)	(17.7)	(69.8)	(21.0)	(44.4)

Note. Standard errors (across participants) appear in parentheses. (D, dominant limb; ND, non-dominant limb).

data are presented in Table 1. The PD patients participated in two sessions. During the first session, the patients were instructed to maintain their normal medication regimen ("On" session). For the second session, the patients skipped their morning medication, allowing the testing to take place at least 12 h after their last medication ("Off" session). At least 1 week elapsed between the two sessions.

Control participants participated in a single experiment session. These participants reported and exhibited no history of neurological damage in a neurological battery performed prior to testing.

This work was approved by the University of California, Berkeley Committee on the Usage of Human Research Participants. Informed consent was obtained from all subjects prior to testing.

2.2. Procedure

Participants were seated in front of a 36-in. high table. Kinematic data were collected with an Ascension Technology miniBIRD magnetic tracking system (136 Hz sampling rate) controlled by a computer which also generated the pacing tones. One $8 \times 8 \times 12$-mm kinematic marker was attached to the tip of the index finger.

A synchronization-continuation paradigm was used for all three tasks. During the synchronization phase a 20-ms tone was played every 550 ms. The tones ceased during the continuation phase.

A template mounted on the table served as a spatial goal for the circle drawing tasks. The template consisted of two circles. One circle was 6 cm in diameter and the subject was instructed to trace this pattern; the other circle was 1 cm in diameter and intersected the larger circle at the point farthest from the subject. For the continuous circle drawing task, the subject was instructed to complete one cycle for every beat of the metronome, moving continuously from cycle to cycle. The finger

tip was to pass through the smaller circle coincident with the metronome beat. For the intermittent circle task, the subject was instructed to trace a complete circle during one 550-ms interval and then pause on the smaller circle for the subsequent 550-ms interval. For the finger tapping task, the subject rested his or her forearm on the table. With the index finger fully extended, the subject was instructed to tap the table coincident with each beat of the metronome. For the tapping task no instructions were given regarding movement continuity. Based on previous studies, we expected that there would be a significant pause between the successive taps.

A trial began when the experimenter triggered the metronome. The subjects were instructed to begin moving in synchrony with the metronome. After 10 paced cycles (5.5 s), the metronome was disengaged and data were collected for an additional 11 s, an interval in which approximately 20 movement cycles could be completed. The end of a trial was signaled by a series of four tones. Five test trials were collected for each hand for each of the three timed movement conditions. Prior to the test trials, three practice trials were completed.

In addition to the neurological exam, maximal movement rate was measured to assess motor competence. In both sessions, maximal tapping rate was measured by having the participant tap on the table surface as fast as possible for 10 s. After some of the participants had been tested, it was apparent that the patients had performed as well as the controls on this task. As a further test, the maximum rate test was also performed with arm movements by six of the control participants, two of the PD patients in the "On" session, and five of the PD patients in the "Off" session. In this condition, participants made arm movements between two targets that were spaced 15 cm apart. The instructions emphasized speed over accuracy. As with the tapping task, data were collected for 10 s. In each session, four trials were collected for each hand on the maximal rate tasks.

Each of the 10 conditions, five tasks by two limbs, was tested in separate trial blocks with the order of the blocks randomized across participants. Patients performed the blocks in the same order in the "On" and "Off" sessions. At the start of each block, the experimenter provided instructions and demonstrated the task for that block. Each session lasted approximately 1 h.

2.3. Data Analysis

Only the data from the continuation phase of the test trials were analyzed. For finger tapping, the beginning of each cycle was defined as the point when the finger touched the table. For both drawing tasks, the beginning of a cycle was defined as the maximum displacement in the *y*-dimension, the point at which the marker was farthest from the subject. The beginning of the pause portion of each intermittent circle cycle was defined as the onset of the plateau in the *y*-dimension. Thus, we were able to partition the intermittent circle cycle into pause and movement time.

3. Results

Trajectories of patient and control performance are presented in Fig. 1. Similar to trajectories produced by unimpaired adults when tapping, the PD patients exhibited a pause between tapping cycles. Furthermore, although not at the instructed ratio (discussed below), there were distinct pauses inserted between cycles in the intermittent circle drawing task. No pause is evident in the trajectories produced during continuous circle drawing. Thus, as expected, the movements of the PD patients are similar to the controls in that tapping and intermittent drawing entail discontinuities, a prerequisite for event-based timing.

3.1. Cycle duration

Mean cycle durations for the timed movement conditions are presented in Table 1. Although, as may be expected, PD patients moved slower than controls on average, this was not a significant difference ($F(1,95) = .36$, $p = .55$) nor were timed movements slower in the "Off" session relative to the "On" session ($F(1,95) = 1.76$, $p = .19$)

Table 1 also lists the movement and pause durations for the intermittent circle drawing task. Overall, the patients and controls were able to approximate the target cycle duration. Note that the goal duration for a complete cycle for the intermittent circle drawing task was 1100 ms (550 ms movement + 550 ms pause). While the overall duration was close to this goal, all of the partic-
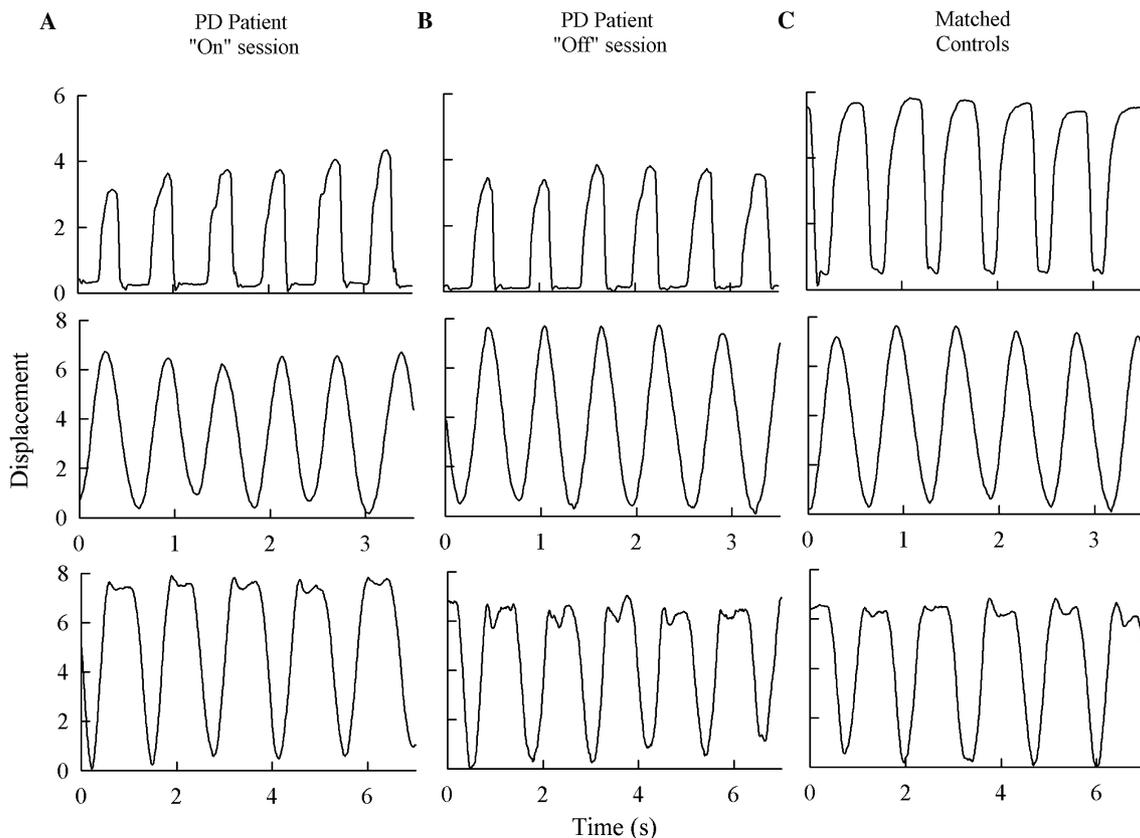

Fig. 1. Kinematic traces as produced by (A) a PD patient in the "On" session, (B) the same PD patient in the "Off" session, and (C) a control.

ipants distorted the target 1:1 movement:pause ratio. The patients performed approximately 3:1 while in the "On" session and 4:1 in the "Off" session. Control participants performed approximately 2.5:1.

3.2. Cycle variability

Of primary interest was the variability of the cycle durations. A normalized measure, the coefficient of variability (CoV), defined as the standard deviation of cycle duration divided by mean cycle duration, was used as illustrated in Fig. 2. The CoV is useful for comparing temporal consistency on tasks with different cycle durations since, within the range studied here, the standard deviation is linearly related to cycle duration (see Robertson et al., 1999). The CoV also accounts for differences in cycle duration between individuals within each task.

3.3. Cycle variability: Parkinson's patients' on- versus off-performance

Our first analysis was the comparison of variability within-subjects, the performance of the patients tested "On" and "Off" medication. Given our interest in seeing if PD produces similar deficits as observed in CE patients, we focused on the two event-based timing tasks, finger tapping and intermittent drawing. A t-test of the combined variability from the intermittent circle drawing and finger tapping tasks was conducted, comparing performance for the "On" and "Off" sessions. There was no difference in performance on these tasks between sessions ($t(7) = -.8518$, $p = .79$). Likewise, a t-test com-

paring performance on the continuous task between the "On" and "Off" sessions was also not significant ($t(7) = -1.30$, $p = .88$).

Previous On–Off comparisons of variability on repetitive movement tasks have only used the tapping task. In the current data set, no difference was found on this task when evaluated alone (dominant limb $t(7) = .23$, $p = .41$; non-dominant limb $t(7) = -1.11$, $p = .85$). This null result is in accord with the previous report of Ivry and Keele (1989), but at odds with that of O'Boyle et al. (1996), who reported increased variability in patients when "off" medication.

3.4. Cycle variability: Parkinson's patients' performance versus controls

Next, we compared temporal variability of the PD patients to controls. While our medication manipulation failed to produce an increase in temporal variability, it is possible that the patients are more variable than appropriately matched control participants. Based on the post hoc observation that the patients were actually more variable when "On" medication, we decided to use the data from this session in the comparisons with the controls. Note that because all of the PD patients were tested in the "On" state first, the two groups have comparable experience with the tasks for these data sets.

No group difference was found on the event-based timing tasks (pooled comparison of tapping and intermittent circle drawing, $t(7) = 1.05$, $p = .16$). We also looked at the tapping data separately given previous research with this task. Although the patients' means were higher than that observed for the controls with both
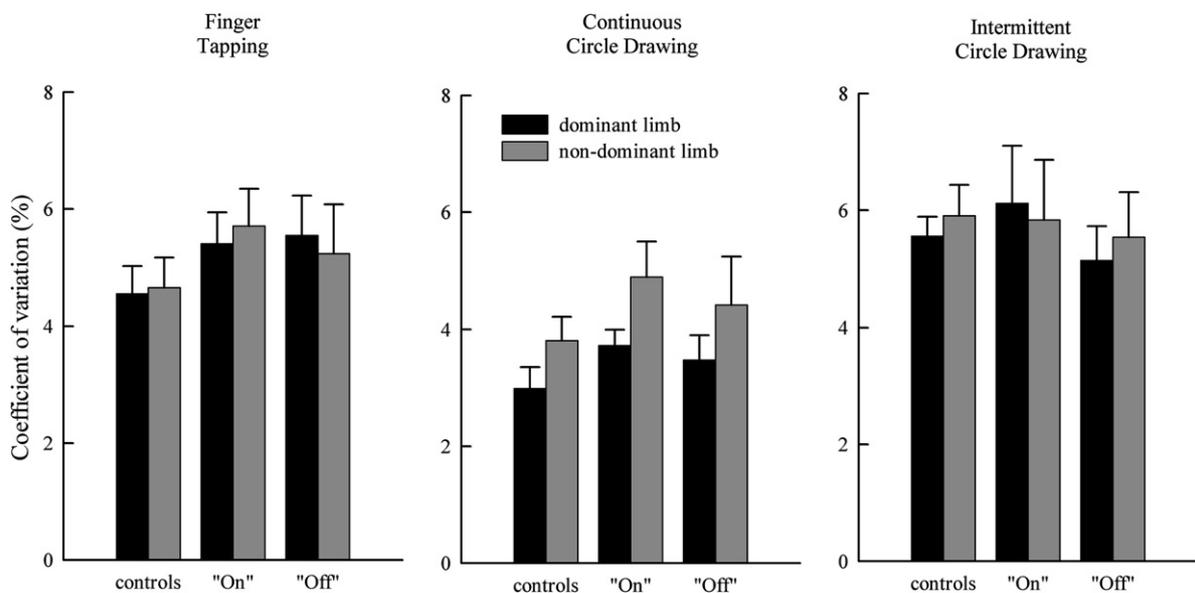

Fig. 2. The average within-subject variability, the coefficient of variation, for all tasks, groups, and sessions. Error bars represent the standard error (the variability in the mean coefficient of variation values across subjects). "On" is performance of PD patients in the "On" session; "Off" is performance of PD patients in the "Off" session.

hands, neither effect was significant (dominant limb $t(7) = 1.13$, $p = .15$; non-dominant limb $t(7) = 1.40$, $p = .10$). Surprisingly, patients tended to be more variable than the controls on the continuous drawing task ($t(7) = 1.70$, $p = .07$), an effect that neared significance.

3.5. Relationship of Parkinson's symptoms to temporal performance

Maximal tapping rate was measured to assess motor competence of the patients in the "On" and "Off" medication sessions. Surprisingly, performance on this task was not mediated by medication state ($F(1,31) = .45$, $p = .51$). Furthermore, the maximal tapping rate for PD patients was greater than that produced by controls ($F(1,31) = 5.13$, $p = .03$). This effect is illustrated in Fig. 3A.

In spite of this, there is evidence that the PD patients in this study exhibited Parkinsonian symptoms. First, the neurological assessments (see Table 2) provide evidence that the patients exhibited mild to moderate impairments. It is regrettable that, due to the limited time of testing in the "Off" session, the neurological assessments were not performed during the "Off" session. However, results from the maximal rate reaching task are reassuring of additive deficits in the "Off" session. When tested on the maximal rate arm movement task, PD patients in the "Off" session were slower than controls ($F(1,21) = 8.92$, $p < .01$; as illustrated in Fig. 3B).

Additional evidence that the patients exhibited Parkinsonian symptoms is evident in the top row of Fig. 1. In the finger tapping task, the task performed without a spatial template, the PD patients produced movements of smaller amplitude than controls. This difference was significant ($t(7) = 4.48$, $p = .001$; as illustrated in Fig. 4).

While the comparison of temporal variability produced by PD patients relative to controls did not reveal a timing deficit associated with PD, disease severity across the patients may predict the variability observed in patient performance. To examine this, Pearson's correlations (one-tailed) were calculated for severity ratings on the UPDRS relative to timing performance. Disease severity did not predict performance on the repetitive tapping task ($r = .41$; $r > .56$ indicates significance a $p < .05$) nor the intermittent drawing task ($r = .18$). However, the UPDRS did predict temporal performance on the continuous drawing task ($r = .72$).

Table 2
Demographic data for the participants.

	PD Patients	Control Subjects
Age (yrs)	65.4 ($SD = 8.2$)	65.0 ($SD = 7.8$)
Education (yrs)	19.25 ($SD = 2.5$)	17.25 ($SD = 2.5$)
Gender (male/female)	5/3	4/4
Years post diagnosis	9.4 ($SD = 5.6$)	
Hoehn and Yahr Scale[a]	Stage 1 = 2	
	Stage 2 = 2	
	Stage 2.5 = 1	
	Stage 3 = 2	
	Stage 3 = 1	
Schwab and England Scale[b]	95% = 2	
	90% = 1	
	80 % = 2	
	70 % = 2	
	65% = 1	
UPDRS[c]	29.8 SD = 19.2	

[a] Hoehn and Yahr (1967).
[b] Schwab and England (1997).
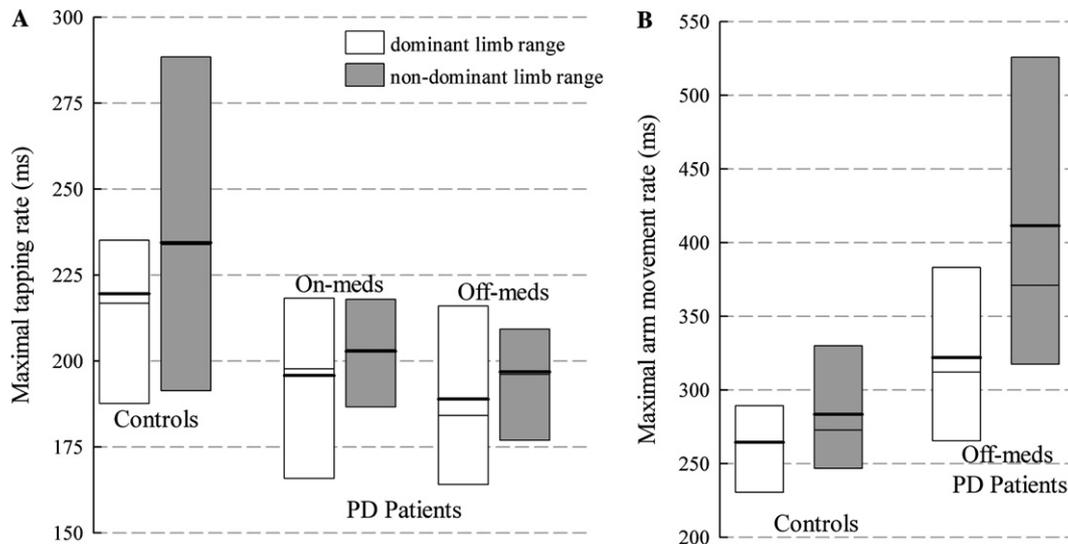[c] Fahn et al. (1987).

Fig. 3. The range of maximal rates produced across groups on the (A) maximal rate tapping task and (B) the maximal rate arm movement task (note that data was not collected on all participants for this task). Thin lines indicate the median within that group/limb; thick lines represent the mean maximal rate.
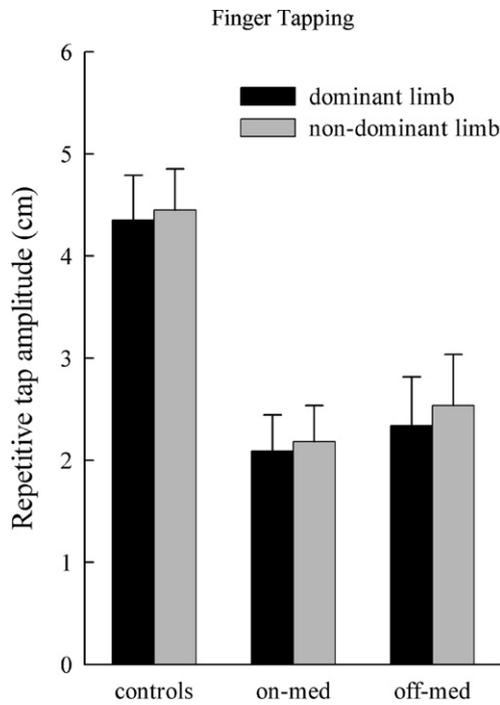
Fig. 4. Average tap amplitude for the timed tapping task.

4. Discussion

In the present study, we examined the performance of PD patients on repetitive movement tasks in which the timing has been hypothesized to be either event-based or emergent. The results clearly indicate that for this group of patients, no deficits were observed on the event-based tasks, finger tapping and intermittent circle drawing. This null finding was obtained in both the "On" and "Off" medication sessions, although as evidenced by the maximum tapping assay, the effects of skipping a medication cycle were minimal, at least for finger movements. For the emergent timing task, continuous circle drawing, the PD patients exhibited a marginally significant increase in variability compared to the controls. As with the event-based tasks, performance did not differ between the "On" and "Off" sessions.

4.1. Comparing the effects of Parkinson's disease and cerebellar lesions

These results stand in contrast to those observed previously in a similar study involving patients with lesions of the cerebellum. As depicted in Fig. 5, cerebellar patients were impaired on the event-based timing tasks (Ivry et al., 2003; Spencer et al., 2003). For patients with unilateral cerebellar lesions, increased temporal variability was observed during finger tapping and intermittent circle drawing when performed with the ipsilesional hand compared to the contralesional hand. In a second study, patients with bilateral cerebellar degeneration were impaired with either hand in comparison to matched controls on tapping and intermittent circle drawing tasks. Critically, in both the unilateral and bilateral cerebellar patients, performance was unimpaired on the continuous circle drawing task.

When considered in conjunction with the current results, two important conclusions can be made. First, the results fail to support the hypothesis that the
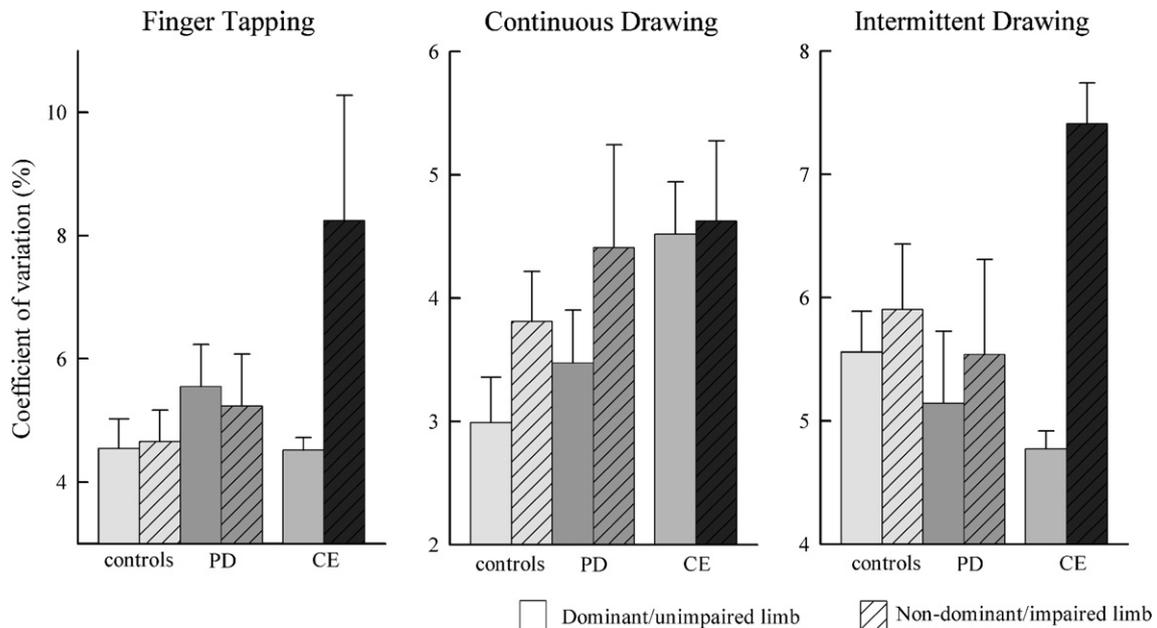

Fig. 5. Comparison of results across patient groups and across studies. CE patients had unilateral damage. Thus the solid lighter-gray bars are for the ipsilesional impaired limb; hatched darker-gray bars are for the contralesional unimpaired limb.

event-based timing tasks are more sensitive to the effects of neurological damage than the emergent timing task. The PD patients were not impaired on the event-based timing tasks, finger tapping and intermittent drawing. Second, the results are consistent with the hypothesis that event-based timing deficits are selective to cerebellar damage, at least for patient groups tested on these two classes of movements. Indeed, the results suggest a possible double dissociation given that the PD patients were marginally impaired on the continuous circle drawing task. This effect requires further study.

4.2. Are Parkinson's patients impaired on tasks requiring precise timing?

While cerebellar patients consistently exhibit increased temporal variability on event-based timing tasks, the picture for PD patients remains unclear. Some studies have reported normal performance on the repetitive tapping task (Duchek et al., 1994) even when the patients are tested off-medication (Ivry & Keele, 1989). The current results are in accord with these studies. However, other studies have reported that PD patients are more variable than controls (Harrington et al., 1998a, 1998b; O'Boyle et al., 1996). There are various reasons for this ambiguous set of results, none of which provide a satisfactory explanation. One possible explanation is that our patients may exhibit less severe deficits relative to those reported by Harrington et al. (1998a, 1998b), O'Boyle et al. (1996) and their respective colleagues. The PD patients in the current study tapped as fast, if not faster than the control participants. Consistent with this, the patients showed little clinical impairment on the UPDRS measures of distal involvement; seven of the PD participants were rated at 0, normal performance, and the other patient was rated at 1, minimal impairment. However, it should be noted that our patients fall within the same range on the UPDRS (mean = 29.8, SD = 19.2) as the patients studied by Harrington et al. (mean = 29.4, SD = 13.6). Furthermore, the reduction in tap amplitude in the PD patients is indicative of a spatial deficit of distal movements in spite of the lack of temporal deficit. This latter note is consistent with research by Margolin and Wing (1983) which suggests that micrographia, reduced writing size, is associated with reduced amplitude or force rather than reduced movement time.

Moreover, the PD patients in the current study did exhibit clinical signs of the disease for more proximal effectors. Six scored 1 or higher on the UPDRS measures of hand and wrist movements (opening and closing of the hand; rapid alternation of the wrist) and the patients were slower than the controls on the maximal arm movement assay. We also observed a significant correlation between disease severity and variability on the continuous circle drawing task and a near significant correlation with variability on the intermittent circle drawing task. These results suggest that, even if our patients exhibited little problem with distal movements, evidence of their Parkinsonism was evident with more proximal movements. Nonetheless, they were not impaired on the intermittent circle drawing task, a task that required movement about the elbow and shoulder. In conclusion, the presence or absence of PD symptoms does not appear to account for whether or not the patients show a timing impairment.

4.3. Event and emergent timing

Three sets of results support the distinction between event-based and emergent timing. First, the correlational studies with neurologically healthy individuals show that a common process underlies temporal acuity on tapping and intermittent circle drawing which is separable from that associated with continuous circle drawing. Individual differences on the two event-based timing tasks are also correlated with the ability to judge the duration of brief events (Zelaznik et al., 2002). Second, in a study of bimanual coordination, split-brain patients exhibit a striking difference in the coordination between the two classes of movements. The two hands remain temporally coupled during tapping (Ivry & Hazeltine, 1999; Tuller & Kelso, 1989) and intermittent finger movements (Kennerley, Diedrichsen, Hazeltine, Semjen, & Ivry, 2002). In contrast, this coupling is absent during continuous circle drawing (Kennerley et al., 2002). Third, patients with cerebellar lesions are selectively impaired on event-based timing tasks. Taken together, these results indicate that the event-based/emergent timing distinction is not only psychologically valid, but that these two classes of movements engage distinct neural systems.

The difference between event-based and emergent timing can also be seen in a micro-analysis of the temporal structure of tapping and continuous circle drawing (Spencer & Zelaznik, 2003). For the tapping task, cycle duration was computed based on the point of table contact, the point of flexion-onset, the point of maximum velocity, and the point of minimum velocity. The variability in cycle time differed greatly depending on the point at which the cycle duration was measured. For circle drawing, when cycle duration was computed based on the reversal point in the *y*-dimension, the reversal point in the *x*-dimension, the point of maximum velocity, and the point of minimum velocity, there was no difference in temporal variability with respect to where the cycle duration was measured. This analysis suggests that timing is an emergent property during such movements, reflecting the continuous variation in a control parameter such as joint stiffness. In contrast, salient events are timed during tapping. The Spencer and Zelaznik study suggests that this salient point is the contact point with

the table surface, consistent with the task instruction to "touch the table coincident with the beat" in the paced portion of the trial.

4.4. Conclusions

In sum, the cerebellum has a clear role in the temporal control of event-based timing and contributes minimally, if at all, to the temporal control of emergent timing. Based on the present results, the basal ganglia appear to contribute minimally to the temporal control of event-based timing (see also, Aparicio and Ivry, this volume). The present results suggest a possible role for the basal ganglia in emergent timing. How timing emerges in continuous movements and the underlying subcortical and cortical neural correlates remains an important problem for future investigation.

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