Neuropsychology
1999, Vol. 13, No. 1, 10–21

0894-4105/99/$3.00

Effects of Divided Attention on Temporal Processing in Patients With Lesions of the Cerebellum or Frontal Lobe

Laurence Casini
Centre National de la Recherche Scientifique

Richard B. Ivry
University of California, Berkeley

Prefrontal cortex and cerebellum have both been implicated in temporal processing tasks although the exact contribution of each system remains unclear. To investigate this issue, control participants and patients with either prefrontal or cerebellar lesions were tested on temporal and nontemporal perceptual tasks under 2 levels of attentional load. Each trial involved a comparison between a standard tone and a subsequent comparison tone that varied in frequency, duration, or both. When participants had to make concurrent judgments on both dimensions, patients with frontal lobe lesions were significantly impaired on both tasks whereas the variability of cerebellar patients increased in the duration task only. This dissociation suggests that deficits on temporal processing tasks observed in frontal patients can be related to the attention demands of such tasks; cerebellar patients have a more specific problem related to timing.

The brain is continually required to process temporal information. This can be seen in all of our everyday activities: coordinating the gestures of a complex action, anticipating the duration of a signal light, or preparing the evening meal—all of these entail a system that is able to anticipate events in advance. Extensive research over the past decade has sought to elucidate fundamental questions concerning how time is represented in the brain. Performance on time perception tasks entails multiple-component operations (Gibbon, Church, & Meck, 1984; Ivry & Hazeltine, 1995; Treisman, 1963). In addition to the ability to represent temporal information, such tasks require perceptual, attentional, and memory processes. There has been substantial interest in the neuropsychological literature on the neural systems involved in the perception and production of relatively short intervals (reviewed in Gibbon, Malapani, Dale, & Gallistel, 1997; Ivry, 1996). Much of this work has focused on the cerebellum, frontal lobe, and basal ganglia. Performance on temporal processing tasks is disrupted following lesions to any one of these three structures (for reviews, see Ivry, 1996; Meck, 1996). What remains to be determined is the functional role for these structures, as well as the interactions between them in the course of temporal processing. In this article, we focus on two of these regions; the prefrontal cortex and cerebellum.

The importance of the frontal lobes in temporal processing has been demonstrated in both animal and human studies. It has been suggested that many of the problems experienced by patients with frontal lesions reflect a problem in the temporal organization of mental and motor activities (Fuster, 1981; Nichelli, Clark, Hollnagel, & Grafman, 1995; Stuss & Benson, 1984). A loss of temporal coherence would obviously be a major impediment to the planning and execution of goal-oriented behavior. For example, frontal patients have difficulty in reconstructing the time sequence of a series of events or in making judgments concerning the temporal order of a series of consecutive stimuli (Mangels, 1997; Milner, Corsi, & Leonard, 1991; Shimamura, Janowsky, & Squire, 1990). These tests assess patients' memories for the temporal relationship between items; that is, for judgments of relative time. They do not explicitly test memory for the duration of temporal intervals, a task that might require the representation of absolute time.

Evoked potential studies in humans have also implicated frontal regions in temporal processing tasks. Elbert, Ulrich, Rockstroh, and Lutzenberger (1991) observed slow cortical potentials over the frontotemporal region when people were required to reproduce a target duration. Similarly, the evoked responses were linked to frontal regions during a duration discrimination task (Bruder et al., 1992). Although these studies based their anatomical conclusions on the relative amplitude of slow cortical potentials, Casini and Macar (1996a, 1996b) used topographical analyses to localize the underlying generators in a more reliable manner. The level of activation over dorsolateral prefrontal regions was found to be predictive of performance on a time reproduction task: Activity level was inversely related to the accuracy of the produced interval.

It has also been proposed that the cerebellum plays a central role in the representation of temporal information.

Laurence Casini, Centre de Recherche en Neurosciences Cognitives, Centre National de la Recherche Scientifique (CNRS-CRNC), Marseille, France; Richard B. Ivry, Department of Psychology, University of California, Berkeley.

This work was supported by National Institutes of Health Grants NS30256 and NS17778 and a postdoctoral fellowship from the Direction des Recherches et Techniques of France. We are grateful to Robert Knight, Robert Rafal, Donatella Scabini, and Naomi Shimizu for their assistance in recruiting, evaluating, and testing the patients and to Eliot Hazeltine and Jennifer Mangels for their comments and criticisms.

Correspondence concerning this article should be addressed to Laurence Casini, CNRS-CRNC, 31 chemin Joseph Aiguier, 13402 Marseille Cedex 20, France. Electronic mail may be sent to casini@lnf.cnrs-mrs.fr.

Support for this hypothesis comes from both empirical study and theoretical analysis of this structure. Braitenberg (1967) hypothesized that the cerebellar cortex implemented an interval-based timing system through a series of delay lines formed by parallel fiber activity. Although further anatomical and physiological analyses questioned the idea of this "hardware" form of timing (Fahle & Braitenberg, 1984), other theorists have suggested that a "software" spectrum of timing elements might emerge through the relatively slow synaptic interactions that take place in the cerebellar cortex (Buonomano & Mauk, 1994; Fiala, Grossberg, & Bullock, 1996). Classical conditioning studies of the eyeblink response have focused on the cerebellum (e.g., Daum et al., 1993b; Thompson, 1990; Woodruff-Pak, Papka, & Ivry, 1996) and stressed the importance of temporal representations (Ivry, 1993). Of relevance here is the fact that the cerebellar cortex is essential for the precise timing that makes this learned response adaptive (e.g., Perret, Ruiz, & Mauk, 1993).

Ivry and his colleagues have looked for more direct evidence of the role of the cerebellum in timing. Patients with cerebellar lesions show increased variability on a repetitive tapping task (Ivry & Keele, 1989), with the deficit attributed to poor timing control rather than motor execution for those patients with lesions in the more lateral regions of the neocerebellum (Franz, Ivry, & Helmuth, 1996; Ivry, Keele, & Diener, 1988). Moreover, cerebellar lesions were associated with poor acuity on perceptual tasks that require precise timing, including duration discrimination (Ivry & Keele, 1989) and velocity discrimination (Grill, Hallett, Marcus, & McShane, 1994; Ivry & Diener, 1991; Nawrot & Rizzo, 1995). Given that these patients do not show perceptual deficits on nontemporal tasks such as loudness or position discrimination, the cerebellar contribution appears to be specific to those tasks that require a precise representation of the fine timing between sensory and motor events.

Neuroimaging studies with positron emission tomography (PET) provide further evidence of prefrontal and cerebellar involvement in temporal processing tasks (as well as basal ganglia). Increases in regional cerebral blood flow were observed in both areas when participants judged the duration of a visual stimulus that ranged in duration from 410 ms to 910 ms, compared with a control condition in which the stimuli were passively observed (Maquet et al., 1996). These results are in agreement with the findings of Jueptner and colleagues (Jueptner, Flerlch, Weiller, Mueller, & Diener, 1996; Jueptner et al., 1995). Compared with a passive stimulus-only condition, activation was greater in both vermal and hemispheric loci when participants were required to judge the duration of intervals marked by auditory signals (Jueptner et al., 1995) and when participants had to judge the velocity of a moving peg on their right hand (Jueptner, Flerlch, Weiller, Meuller, & Diener, 1996). In both studies, increased activity was also observed in dorsolateral prefrontal cortex.

To date, comparisons between the cerebellum and frontal cortex on temporal processing tasks have generally been indirect. The rat model of internal timing has focused on the striatal-frontal-hippocampal pathway, and the cerebellum has not been included in the various lesion and pharmacological manipulations (Gibbon et al., 1997). Within the human neuropsychological literature, there have been substantial differences in methodology between studies assessing cerebellar and frontal contributions on timing tasks (Ivry & Keele, 1989; Von Steinbuchel, Wittman, & Poeppel, 1996). Moreover, between the human and animal literatures, the dependent variables have been quite different. The rat studies have focused on how lesions or pharmacological agents alter perceived duration, or bias, whereas the human cerebellar studies have focused on changes in the consistency of an internal timing system.

Mangels, Ivry, and Shimizu (1998) recently reported a direct comparison of patients with either cerebellar or prefrontal lesions on a series of perceptual tasks. In their first experiment, the performance of frontal and cerebellar patients was compared on two duration discrimination tasks, one with intervals centered around 400 ms and the other with intervals centered around 4 s. The goal was to test the prediction that the cerebellar timing system was limited to relatively short intervals, those relevant for motor control, whereas the contribution of prefrontal cortex would become manifest at longer intervals. The results, however, only provided support for the latter prediction. Compared with healthy control participants, the cerebellar group was impaired on both duration discrimination tasks, suggesting that this area was essential for the accurate representation of temporal information across both interval ranges. In contrast, the frontal group was only impaired on the 4-s version of the task, consistent with the hypothesis that this region is essential for sustaining the information over a longer period of time. Further support for this hypothesis was obtained in a second experiment in which participants were required to compare the frequency of two stimuli with either a 1-s or 4-s interval separating the standard and comparison tones. Only the frontal patients showed a decrease in performance when the interstimulus interval was extended. These results are consistent with the idea that the cerebellum is essential for providing an accurate representation of temporal information whereas the contribution of prefrontal cortex is best characterized in terms of a central role in working memory.

The Mangels et al. (1998) study provides an initial step toward dissociating the specialized roles of the cerebellum and the prefrontal cortex in temporal processing tasks. Although their results indicated that the cerebellum plays a critical role in representing temporal information, the integrity of the prefrontal cortex was also found to be important, especially when either temporal or nontemporal judgments were required for stimuli extending over intervals of several seconds. In the present study, we varied the attentional load during temporal and nontemporal perceptual tasks given that such manipulations have been shown to influence both acuity and subjective duration in time perception experiments (e.g., Macar, Grondin, & Casini, 1994; Zakay, 1989; reviewed in Brown, 1997). Patients with either cerebellar or prefrontal lesions were required to perform duration and frequency discrimination tasks, either in isolation or in tandem. We hypothesized that patients with prefrontal lesions would show the greatest impairment in the dual-task conditions, reflecting the role of prefrontal cortex in the allocation of attentional resources. In contrast, patients with cerebellar lesions were expected to exhibit similar attentional costs as control participants on the frequency discrimination task. Demonstrating that the prefrontal patients are disproportionately sensitive to the attentional requirements in these tasks would provide further evidence that the cerebellum and prefrontal cortex make dissociable contributions to temporal processing tasks.

Method

Participants

Three groups of participants were chosen: patients with frontal lobe lesions, patients with cerebellar lesions, and healthy controls (Table 1). The patients were recruited with the assistance of members of the Neurology Department at the Veterans Administration Medical Center in Martinez, CA. The patients were initially identified through a review of computerized tomography (CT) and magnetic resonance imaging (MRI) records indicating a lesion involving either lateral prefrontal cortex or the hemispheric regions of the cerebellum. Their medical records were then reviewed. Exclusion criteria included any past psychiatric disorders or significant medical problems related to other neurological events. All patients meeting these criteria were given a neurological and neuropsychological assessment.

Control group. Ten healthy, elderly people (8 men and 2 women) served as a control group. They were recruited from the patient and volunteer population at the Veterans Administration Medical Center, Martinez, CA. They were matched to the patients with respect to age (M = 65.2, SD = 5.2) and education level (M = 14.2, SD = 1.3).

Patients with frontal lobe lesions. Five patients with unilateral lesions of frontal lobe were recruited. The patients had had a single cerebral infarct in the dorsolateral prefrontal region (Figure 1). The patients averaged 69 years of age and 13.4 years of education. The average lesion volume, estimated from quantitative analyses from CT scans, was 61.3 cm^3. The lesion was in the left hemisphere in 4 of the patients. Three of the patients with left hemisphere damage presented some evidence of aphasia in terms of dysfluency and word finding problems. These problems were relatively mild for 2 of the patients and severe for the remaining patient (J.C.). The aphasic problems, however, did not interfere with the patients' abilities to report their perceptual judgments in the current experiment.

Patients with cerebellar damage. Eight patients with lesions of the cerebellum were recruited. Their mean age was 61.3 years and they had an average of 12.1 years of education. Seven patients had unilateral lesions due to either stroke or tumor (Figure 2). Estimates of lesion volume were not available. The lesion was restricted to the left cerebellar hemisphere for 3 patients and to the right hemisphere in the other 4 patients. The lesions appeared to extend into the dentate nucleus for 4 of the patients with unilateral lesions (J.D., E.C., R.M., T.R.). The remaining patient had extensive cerebellar atrophy. The atrophy could be seen in an MRI at all levels of the cerebellum with relative sparing of the anterior lobe. This pattern is consistent with a diagnosis of sporadic cerebellar atrophy and argues against alcohol-based atrophy.

Motor dysfunction of cerebellar patients was estimated by a neurologist using a clinical evaluation testing posture, gait, eye movements, and volitional movements. A 5-point scale ranging from 0 (*no evidence of cerebellar dysfunction*) to 4 (*severe cerebellar dysfunction*) was used. Overall clinical rating of motor signs ranged from 0 to 2.5 (*moderate*). The relatively modest

Table 1
Patient Information and Individual Performance Scores on the Neuropsychological Assessment Tests

		Lesion					WAIS–R					WCST	
Participant	Sex	Side	Vol. (cm^3)	Clin.	Age	Education (years)	Info	Voc	Digit Span	Digit Sym	F, A, S	Cat	Pers. errors (%)
Frontal													
O.A.	M	L	17.5		64	14	12	12	10	11	29	1	25.8
R.M.	M	L	10.3		64	12	8	7	11	10	24	6	13.8
J.C.	M	L	102.6		71	16				10	7	6	17.0
A.L.	F	L	51.2		67	13	13	11	5	7	21	4	28.1
E.B.	F	R	17.3		79	12	10	9	11	15	48	4	25.0
Cerebellar													
M.B.	M	L		0.5	34	12	9	11	10	9	41	6	10.8
J.D.	M	L		2.0	52	12	8	10	15	6	22	6	14.5
T.K.	M	L		0.0	76	3	9			5	19	2	26.6
E.C.	M	R		2.5	60	16	12	15	11	10	33	6	9.0
J.L.	M	R		1.0	69	10	7	9	9	7	26	2	53.1
R.M.	M	R		2.5	54	16	11	13	11	6	25	6	11.2
T.R.	M	R		1.5	71	16	16	19	11	10	24	6	20.2
B.H.	M	Bilat			74	12	9	13	15	7	34	4	28.9
Control[a]	8M, 2F				65	14	13	13	13	13	44	5	17

Note. Vol. (frontal patients only) = volume of lesion estimated from computerized tomography scans; Clin. (cerebellar patients only) = overall clinical rating of motor signs, ranging from 0 (*no impairment*) to 4 (*severe impairment*); WAIS–R = Wechsler Adult Intelligence Scale—Revised (Wechsler, 1987); Info = Information subtest; Voc = Vocabulary subtest; Digit Sym = Digit Symbol subtest; F, A, S = total number of words produced in 3 min on the F, A, S Letter Verbal Fluency Test (Benton & Hamsher, 1978); WCST = Wisconsin Card Sorting Test (Grant & Berg, 1948); Cat = categories attained; Pers. errors = perseverative errors; M = male; F = female; L = unifocal lesion on the left hemisphere; R = unifocal lesion on the right hemisphere; Bilat = lesion on both hemispheres.
[a]The data shown here for control participants are averages.

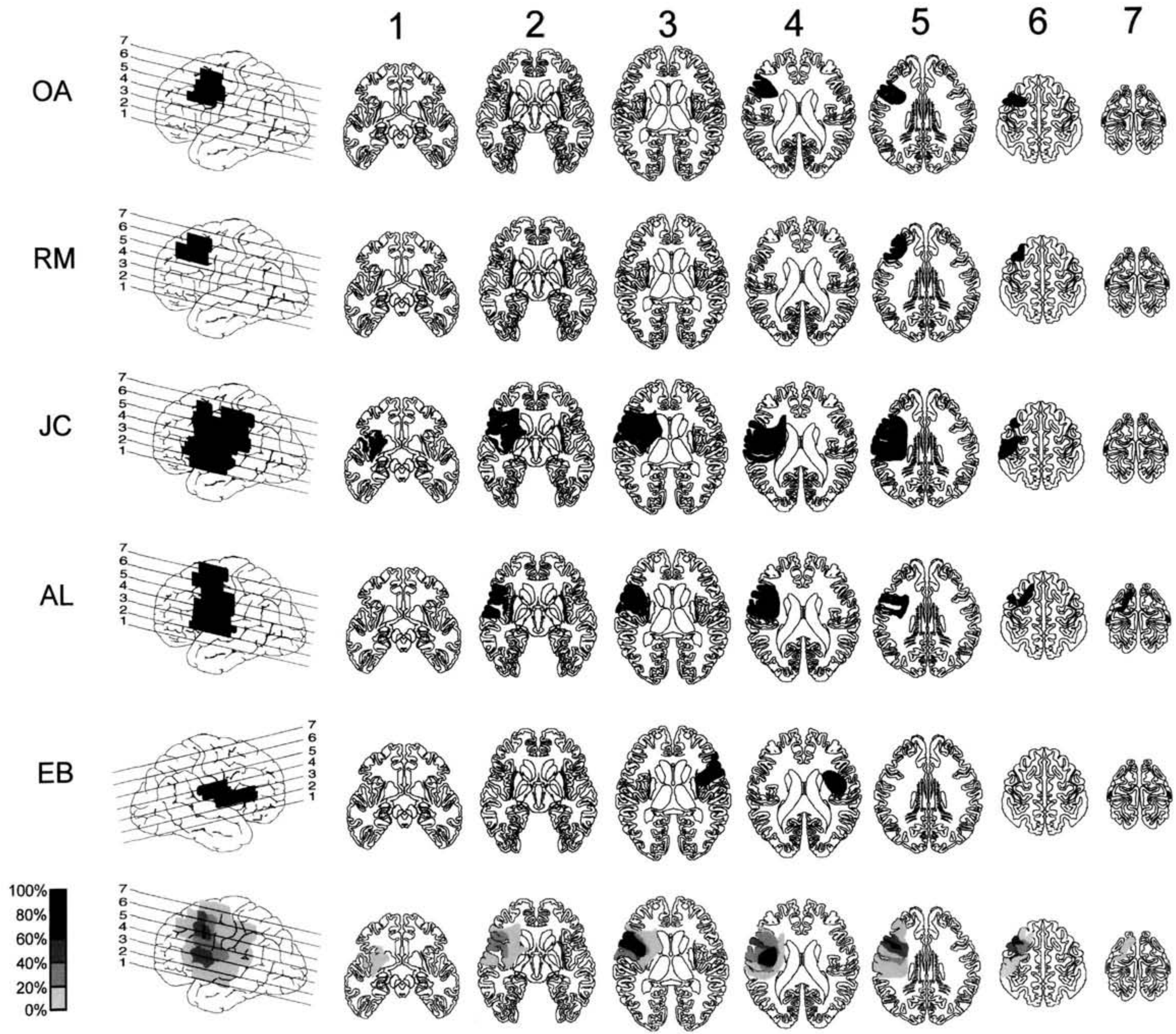

Figure 1. Lesion reconstructions for the 5 patients with frontal lesions. Each row shows a series of seven slices, going inferior to superior from left to right. The bottom row shows a composite of the frontal lesions.

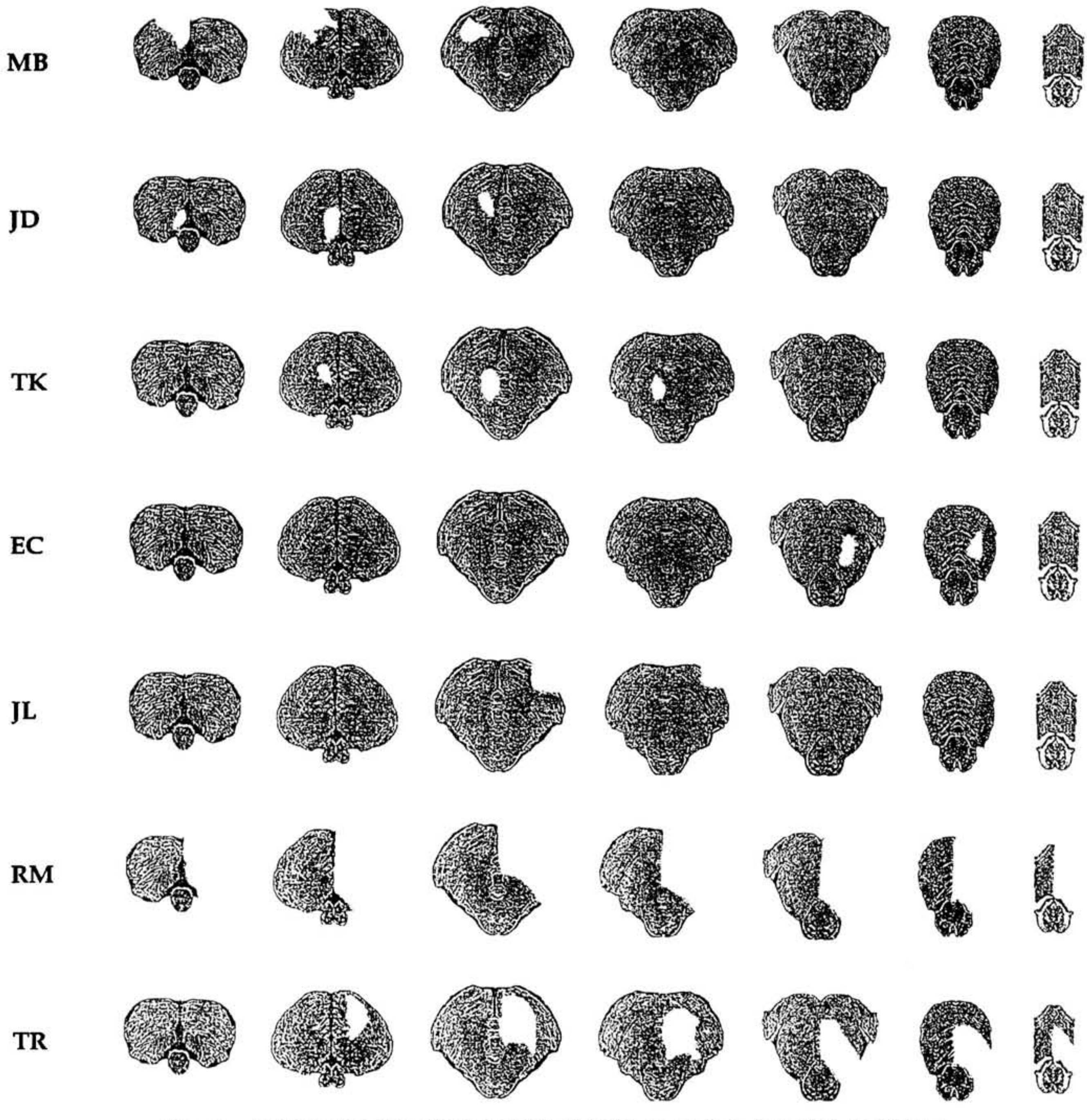

Figure 2. Lesion reconstructions for the 7 patients with focal cerebellar lesions. Each row shows a series of seven slices, going inferior to superior from left to right.

degree of motor dysfunction is likely due to the fact that the clinical evaluation and testing occurred after an extended recovery period of at least 1 year (and over 5 years for most of the patients).

The neuropsychological assessment showed comparable performance between the patients and control participants on all but two tests. The patients performed worse than the controls on the Digit Symbol subtest of the Wechsler Adult Intelligence Scale—Revised (WAIS-R; Wechsler, 1987), $F(2, 19) = 6.76$, $p < .01$, and the Verbal Fluency Test (FAS; Benton & Hamsher, 1978), $F(2, 19) = 5.82$, $p < .01$. The only test revealing a difference between the patient groups was the Digit Symbol test, $t(11) = 2.3$, $p < .05$, with the cerebellar group performing more poorly than the frontal group. There is considerable debate at present as to whether cerebellar lesions produce impairments on tasks designed to assess general and specific aspects of cognitive function (Akshoomoff, Courchesne, Press, & Iragui, 1992; Daum et al., 1993a; Helmuth, Ivry, & Shimizu, 1997), and this issue is outside the focus of this article. However, it is noteworthy that the cerebellar patients were impaired on the two tasks in which speeded performance was required in addition to accuracy.

Given that the focus of this article is on attentional factors, it is important to note that none of the patients had any signs of attentional disorders as assessed by standard clinical procedures. There was no evidence of neglect or extinction and none of the patients had obvious impairments of concentration or vigilance.

Procedure

Each participant was tested individually and completed three blocks of trials. Two of these were single-task (ST) blocks in which the participants judged either the duration or the frequency of the auditory stimuli. In the third block, the dual-task (DT) condition, the participants were required to judge both the duration and the frequency of the stimuli. All of the stimuli were generated by a PC computer and played over the internal speaker of the computer.

All of the tasks used a psychophysical procedure, Parameter Estimation By Sequential Testing (PEST), developed by Taylor and Creelman (1967) and extended by Pentland (1980). Two stimuli are presented on each trial, a standard and a comparison. The procedure is designed to estimate the difference threshold required for participants to accurately judge the comparison on approximately 90% of the trials (corresponding to 1.5 *SD* units on the logit distribution). The procedure is generic in that it can be used with any stimulus dimension. In the current study, we either manipulated the duration, the frequency, or both dimensions of the comparison stimulus. The PEST procedure is adaptive in that it continually uses the information obtained in previous trials in its estimate of the threshold. Specifically, the test stimulus on each trial is the current estimate of either the lower or upper difference threshold. Initially, this estimate is set to a single value for all of the participants. However, on the basis of individual performance, the difference between the standard and comparison will either become smaller or larger. In effect, the PEST procedure creates a situation in which the subjective experience for all participants is approximately equal. The adaptive procedure selects values so that the participant is correct on about 90% of the trials, with the values individually adjusted on the basis of each person's acuity.

Threshold estimates were bidirectional: for the duration discrimination task, independent measures were made for both the short and long thresholds, and for the frequency discrimination task, independent measures were made for both the lower and higher thresholds. The final estimates were based on 30 trials of each threshold, or a total of 60 trials per block. Computer simulations have demonstrated that the PEST procedure is both efficient and stable (Madigan & Williams, 1987; Pentland, 1980). With 30 trials per threshold, the procedure is likely to converge on the correct estimate over a wide range of starting values.

Duration perception task. The standard stimulus was a 600-Hz tone, presented for a fixed duration of 400 ms. After a 1-s interstimulus interval, the comparison was presented. The frequency of the comparison stimulus was fixed at 600 Hz, but the stimulus varied in duration. Participants were instructed that the first tone was the standard and that they were required to judge the duration of the comparison tone. On each trial, participants judged whether the second tone was shorter or longer than the standard and gave their responses verbally (*short* or *long*). The experimenter entered the response on the keyboard and the computer then determined the test value for the next trial. To reduce the computational process, the logit distribution was divided into 61 equal steps with 6 ms between each step (range of comparison values: 220 ms–580 ms).

Frequency perception task. The general procedure was identical to that used in the duration task except that the second tone varied in frequency rather than duration. The standard tone was again a 600-Hz tone, presented for 400 ms. The duration of comparison tone was also fixed at 400 ms, but now its frequency was varied. Participants judged the frequency and gave their response verbally (*up* or *down*). Each of the 61 steps were separated by 1 Hz (range of comparison values: 570 Hz–630 Hz).

Dual task. In the dual-task block, both the duration and frequency of the comparison stimulus were varied. On each trial, participants first heard the standard stimulus (600 Hz, 400 ms), followed after a 1-s interstimulus interval by the comparison stimulus. Separate PEST procedures were used to make independent estimates for the two comparison values; pilot testing indicated that there were no consistent biases for one response to be linked to another (e.g., participants to be more likely to say *shorter* when they heard a high frequency tone). Participants had to give two responses on each trial, one indicating the duration of the comparison tone (*shorter* or *longer*) and a second indicating the frequency of the comparison tone (*up* or *down*). Participants were free to make the two judgments in whichever order they preferred. The range of comparison values was the same as in the single task conditions.

Order of tasks. The three blocks were completed in a single 1-hr session. The single tasks were always performed first, with the order of the duration and frequency tasks counterbalanced across participants. The dual task was always performed last. This not only made it easier for the participants to understand the requirements in this condition, but it also increased the likelihood that the participants would not attend to both dimensions in the single task conditions. Although this ordering introduces a confound when comparing single- and dual-task performance, our primary interest involves a single-dual comparison between the three groups of participants.

Results

The dependent variables in this experiment were the measures of perceptual acuity and bias provided by the PEST procedure. *Acuity* was operationalized as the difference between the upper and lower difference threshold estimates divided by three. This measure corresponds to 1 standard deviation unit, measured in ms for the duration discrimination task and in Hz for the frequency discrimination task. Larger standard deviations indicate that a greater difference was required between the standard and comparison values in order to meet the criterion level of performance. The point of subjective equality (PSE) was taken as the measure of bias and corresponded to the midpoint between the two thresholds. This corresponds to the value at which participants were equally likely to respond shorter and up or longer and down. In the duration discrimination task, a PSE greater than the standard of 400 ms indicates that the comparison duration was underestimated. More time must elapse for the comparison to be judged equal in duration to 400 ms. In the frequency discrimination task, a PSE greater than the standard of 600 Hz indicates that the comparison frequency was underestimated. The frequency of the comparison must be higher to be judged equal to the standard.

Analyses of variance (ANOVAs) were done on the two indices. One variable was group (controls, cerebellars, and frontals) and the other variable was condition (single or dual task). Because the units are not comparable on the two tasks, separate analyses were conducted on the duration and frequency data.

Duration Perception Task

Standard deviation. Figure 3A shows the mean standard deviation scores for each group of participants in the ST and DT conditions. In both conditions, the values are higher for the cerebellar and frontal groups in comparison to the control participants, $F(2, 20) = 5.16, p < .01$. For the target criterion, the patients required a larger difference in duration between the standard and comparison tone. There was no difference between the two patient groups. The comparison between the ST and DT conditions shows that performance was poorer in the dual-task condition, $F(1, 20) = 19.90, p < .0001$. The percent increase in the difference threshold was 29%, 41%, and 24% for the controls, cerebellars, and frontals, respectively. Although the increase was greatest for the cerebellar patients, the Group × Condition interaction was not significant, $F(2, 20) = 2.10$.

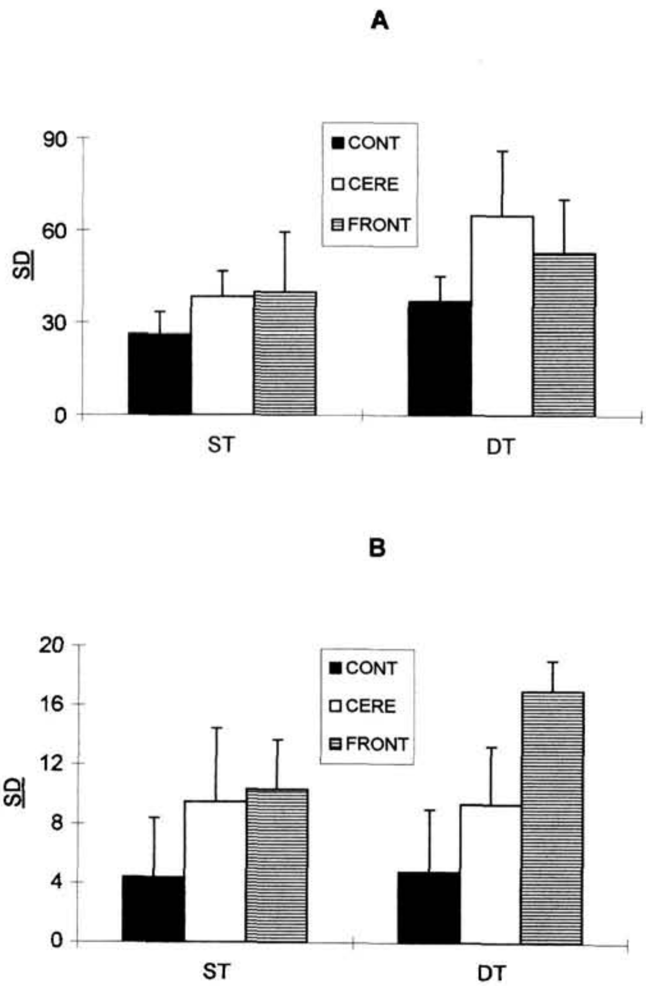

Figure 3. Difference threshold estimated as 1 *SD* of the psychometric function on the duration (A) and frequency (B) tasks in the single- and dual-task conditions (ST and DT, respectively). Error bars reflect 95% confidence intervals around each mean. CONT = controls; CERE = cerebellar lesions; FRONT = frontal lesions.

Table 2
Individual Difference Thresholds on Duration and Frequency Tasks in the Single- and Dual-Task Conditions

	Duration (ms)		Frequency (Hz)	
Patient	ST	DT	ST	DT
Frontal				
O.A.	22	52	7	16
R.M.	44	50	9	17
J.C.	38	60	10	15
A.L.	64	70	11	18
E.B.	32	32	14	19
Cerebellar				
M.B.	36	38	2	4
J.D.	44	66	16	13
T.K.	58	76	18	12
E.C.	18	24	5	9
J.L.	38	44	14	16
R.M.	46	82	15	11
T.R.	36	80	4	4
B.H.	34	116	11	14

Note. ST = single-task condition; DT = dual-task condition.

Table 2 presents the difference thresholds for each of the patients individually. As can be seen, there is considerable overlap between the scores for the cerebellar and frontal patients. Three additional points are noteworthy. First, although the sample size was small, there was no clear difference between the patients with focal left-sided cerebellar lesions (M.B., J.D., T.K.) and those with right-sided cerebellar lesions (E.C., J.L., R.M., T.R.). Second, the difference threshold increased most sharply for the patient with bilateral cerebellar atrophy (B.H.). Atrophy patients tended to perform more poorly than the patients with unilateral lesions in a previous study of time perception (Ivry & Keele, 1989). Third, the only patient who failed to show any increase in the DT condition was the 1 patient with right-hemisphere prefrontal damage (E.B.).

PSE. The mean PSE values are presented in Table 3. There was no significant difference between the three groups on this measure, $F(2, 20) < 1$. All of the means were longer than the target duration of 400 ms, indicating that the participants consistently showed a bias to underestimate the duration of the comparison stimulus. Although the mean PSEs were larger in the dual-task condition, this effect was only marginally significant, $F(1, 20) = 2.83, p < .10$. The Group × Condition interaction was not significant, $F(2, 20) < 1$.

Frequency Perception Task

Standard deviation. The mean standard deviation scores on the frequency task are shown in Figure 3B. In both conditions, the patients performed more poorly than the control participants, $F(2, 20) = 6.49, p < .01$. The main effect of condition, $F(1, 20) = 17.56, p < .001$, and the interaction, $F(2, 20) = 13.47, p < .0001$, were significant. In the single-task condition, both groups of patients showed

Table 3
Means and Standard Errors for Point of Subjective Equality (PSE) Obtained in Single- and Dual-Task Conditions on Each Task for the Three Groups

	Control		Cerebellar		Frontal	
Task	*M*	*SE*	*M*	*SE*	*M*	*SE*
Duration (ms)						
ST	423.7	9.5	419.9	15.2	440.8	4.9
DT	441.1	13.6	441.6	15.4	448.0	9.6
Frequency (Hz)						
ST	599.9	0.8	600.1	2.6	604.7	2.0
DT	598.9	1.6	596.1	2.7	598.1	2.0

Note. ST = single-task condition; DT = dual-task condition.

poorer acuity than the controls, and the two groups did not differ from one another, $F(1, 11) < 1$. On the dual-task block, both groups of patients were also impaired relative to the controls, but here the frontal patients performed significantly worse than the cerebellar patients, $F(1, 11) = 9.84$, $p < .01$.

Of central interest is the fact that only the frontal lobe patients showed a significant decrease in performance between the single- and dual-task conditions on the frequency task, $t(8) = -4.67$, $p < .005$. The dual-task performance of the controls, $t(18) = 0.87$, and the cerebellars, $t(14) = 0.93$, on the frequency task was comparable to that found under single-task conditions. A post hoc analysis restricted to the two patient groups revealed a significant Group $\times$ Condition interaction, $F(1, 11) = 16.20, p < .005$. Whereas all groups showed an increase in the duration difference threshold under dual-task conditions, only the frontals showed a concomitant increase in the frequency difference threshold. The percentage increase in the difference threshold for the controls, cerebellars, and frontals was 9%, 0%, and 39%, respectively.

The difference thresholds for each patient on the frequency task are shown in Table 2. The effect of the DT condition on the two groups is quite striking. All 5 of the frontal patients showed an increase in the DT condition, and the increase ranged from 5 Hz to 9 Hz. In contrast, the difference threshold was larger in the DT condition for only 4 of the 8 cerebellar patients, and here the increase was never greater than 3.33 Hz. In terms of the difference between the ST and DT conditions, there was no overlap between the two groups of patients.

PSE. The PSE values on the frequency task are shown in Table 3. The effect of condition was significant, $F(1, 20) = 10.39$, $p < .005$. All groups judged the comparison tone as higher in frequency when they were in the dual-task condition. There was no significant difference between groups on this measure, $F(2, 20) < 1$, nor was the interaction significant, $F(2, 20) < 1$.

Discussion

Previous research has shown that lesions to the frontal lobes or cerebellum can impair performance on time-perception tasks. However, it has been difficult to identify functional dissociations because of differences in methodology, dependent variables, and the lack of direct comparisons. In this experiment, we compared performance on a temporal and nontemporal task as a function of attentional load. Different patterns of interference were observed for the two patient groups, providing an important step in understanding how the cerebellum and frontal lobe may make differential contributions to tasks that require temporal processing.

The single-task results did not reveal any differences between the patient groups. The cerebellar group was more variable on the duration discrimination task in comparison to the control participants, thus replicating previous results (Ivry & Keele, 1989; Mangels et al., 1998). However, unlike the results of Mangels et al., the frontal patients were also impaired on this task in the present study. Both of the patient groups were also impaired on the frequency perception task under single-task conditions.

The poor performance on the frequency discrimination task was unexpected. This task was intended to serve as an auditory control task. The patients may be more variable than controls on any psychophysical task, reflecting generalized problems in performing these relatively demanding tasks. For example, such tasks require that the participants concentrate for sustained periods of time because a block of trials lasts for approximately 8 min. This may be more difficult following brain damage.

On the other hand, it is possible that these deficits reflect specific problems in making auditory discriminations. Anatomical studies in the monkey have shown that secondary auditory-association areas innervate Area 46 of prefrontal cortex (Pandya & Seltzer, 1982). Similarly, the cerebellum receives auditory inputs. In the rat, auditory regions of the cortex project to the parafloccular lobule of the cerebellum through both the mossy and the climbing fiber pathways (Azizi, Burne, & Woodward, 1985), and subcortical projections to the cerebellar vermis have also been shown by electrical stimulation of the inferior colliculus (Huffman & Henson, 1990). Moreover, in eyeblink conditioning studies, an auditory tone is frequently used as the conditioning stimulus and numerous studies have demonstrated that this signal is projected through mossy fibers (Steinmetz et al., 1987; reviewed in Thompson, 1990). It is possible that the frequency-perception problems occur as a result of damage to representations of auditory signals in either prefrontal or cerebellar regions. However, the functions of tuning to pure tones of cerebellar neurons in the auditory projection region of the vermis in the cat are quite broad (Aitkin & Boyd, 1975). Individual neurons respond at a relatively constant rate over a range of several octaves, making it unlikely that they could support the fine discrimination capability required on the frequency task. We are unaware of similar studies of prefrontal neurons. Future studies will be required to examine these different hypotheses. It is, of course, possible that the frontal and cerebellar groups perform poorly on this task for different reasons.

More relevant to the focus of this experiment, the dual-task condition revealed an important difference in performance between the two patient groups. When the attentional load was increased by requiring simultaneous judgments of duration and frequency, all three groups became more variable on the duration discrimination task. This result is consistent with numerous results obtained with healthy participants indicating that temporal judgments can be influenced by attentional manipulations (Casini & Macar, 1997; Macar et al., 1994; Zakay, 1989). In contrast, only the patients with prefrontal lesions showed a dual-task cost on the frequency discrimination task. The difference threshold increased for all 5 patients in this group under the dual-task condition. The Group $\times$ Condition interaction was significant when the comparison was made between all three groups as well as when the analysis was restricted to the two patient groups. The latter analysis is especially important given the fact that both the cerebellar and frontal patients were more variable than the controls in the single-task conditions.

Although we had predicted that the frontal patients would show the greatest decrement in performance in the dual-task condition, we had anticipated that all of the groups would show some cost during the dual-task block on both tasks. The failure to find any change in performance on the frequency perception task for the control and cerebellar group likely reflects a lack of sensitivity in this task. The effect of attention load was also found to be greater on a temporal task compared to a nontemporal task in a study done by Macar et al. (1994). Nonetheless, this does not compromise the primary finding showing a dissociation between the cerebellar and frontal groups in terms of the effects of dividing attention between the two tasks.

This dissociation allows us to develop hypotheses concerning how the cerebellum and prefrontal cortex contribute to these tasks. It is possible that the prefrontal lesions produced separate disturbances in separable processing systems, one related to time perception and another related to frequency perception. However, a more parsimonious interpretation is that the frontal lesions disrupt attentional processes required in these tasks. Whenever the attentional demands of a task are increased, patients with prefrontal lesions are challenged, regardless of whether the task requires temporal or nontemporal processing. The cerebellar group, on the other hand, did not show a generalized attentional problem.

Courchesne and colleagues (Courchesne et al., 1994; Akshoomoff, Courchesne, & Townsend, 1997) have proposed that the cerebellum plays a critical role in shifting attention. The basic idea here is that, analogous to its role in motor coordination, the cerebellum is essential for mental coordination by orienting perceptual systems to task-relevant stimuli. The primary evidence in support of this hypothesis has come from a divided attention task in which participants must alternate between attending to one of two dimensions (Akshoomoff & Courchesne, 1992; Courchesne et al., 1994). However, Ravizza and Ivry (1998) found that the attentional problem appears to be related to the fact that this task requires rapid successive responses. When the attentional requirements are held constant but the motor demands are reduced, patients with focal cerebellar lesions show a significant improvement in performance. The current results provide further evidence that the deficits observed on perceptual tasks in patients with cerebellar lesions are not related to an attentional problem.

We interpret the cerebellum deficit on the duration discrimination task as further evidence of the role of this structure in representing temporal information. The cerebellum has been shown to be essential for controlling the precise timing in both motor control (e.g., Hore, Wild, & Diener, 1991) and sensorimotor learning (Perret et al., 1993). Together with the perceptual problems shown by cerebellar patients on temporal tasks (Grill et al., 1994; Ivry & Diener, 1991; Ivry & Keele, 1989; Nawrot & Rizzo, 1995), the timing hypothesis provides a theoretical umbrella for these disparate results (see Ivry, 1996). Recent theoretical conjectures have centered on the idea that timing within the cerebellum consists of a set of distributed functional units tuned to different temporal intervals (Buonomano & Mauk, 1994; Fiala et al., 1996; Ivry, 1996). For example, Buonomano and Mauk propose that the coding of duration could emerge from relatively slow synaptic interactions occurring in the cerebellar cortex. Different temporal intervals would be coded through negative feedback loops involving the interaction of granule and Golgi cells on Purkinje cells. Models such as these assume that temporal information is transformed into a spatial code (see also, Fiala et al., 1996). Lesions would be expected to add noise to the system, which would be reflected as increased variability on the duration discrimination tasks in the current study.

However, the cerebellar timing system is only one functional component required for these tasks. Successful performance also depends on other operations such as those involved in attention, memory, and decision processes. There are obviously a number of ways in which an attentional process would be required for successful performance on these difficult discrimination tasks. In the single-task condition, the participant would want to focus on the task-relevant dimension. The prefrontal cortex has been hypothesized to assist in such filtering operations, perhaps by attenuating information from irrelevant information channels (Knight, 1994). Different anatomical and neuroimaging studies have revealed projections from the neocerebellar cortex to the prefrontal cortex (Middleton & Strick, 1994). Thus, the increased variability in frontal patients on the duration perception task could be viewed as a manifestation of a failure to fully attend to the temporal information provided by the cerebellum. The increased variability observed in the prefrontal patients on both tasks in the dual-task condition would be consistent with a putative role for this neural region in coordinating processing across different processing systems (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991).

The relationship between working memory and attention remains unclear (see Shimamura, 1995). In the present study, we have emphasized the attentional role of lateral prefrontal cortex. However, a functional account of this region could also be stated in terms of decision or memory processes. Our psychophysical procedure requires a comparison between two successive stimuli, separated by a 1-s interval. A representation of the standard stimulus would have to be maintained across the interstimulus interval as well as during the presentation of the comparison, at least until a decision is reached. Such an operation would fit with the working memory operations associated with lateral prefrontal cortex (Goldman-Rakic, 1992). As noted earlier, Mangels et al. (1998) found that the performance of patients with prefrontal lesions was especially sensitive to the delay between the offset of the standard and the offset of the comparison. These patients, many of whom were in the current study, showed an increase in variability as this interval was lengthened, an effect observed on both duration and frequency discrimination tasks. At present, we can conclude that the contribution of prefrontal cortex to performance on these tasks becomes more pronounced as the task becomes more difficult, either through the dual-task manipulation or by extending the temporal extent of the stimulus events.

Over the past decade, an extensive literature has emerged exploring the neurological correlates of the hypothesized component operations involved in temporal processing tasks (for recent reviews see Gibbon et al., 1997; Ivry, 1996; Meck, 1996). In the scalar timing theory (Church, 1984), the basic component of timing is a pacemaker that produces outputs, called pulses, at a given rate. These pulses are kept in a counter gated by a switch. A comparator process contrasts the value accumulated in the counter with values that have been stored in reference memory on previous trials. Responses are determined on the basis of this comparison.

Research on the basal ganglia has implicated this subcortical structure as a key component of an internal pacemaker (Meck, 1996; Gibbon et al., 1997). Executive and memory processes have been associated with cortical processes, including a putative role of frontal cortex in an attentional system required to monitor the output of the timing system (Olton, Wenk, Church, & Meck, 1988). Although the current data are in accord with this latter hypothesis, we have postulated a central role for the cerebellum in the clock process, the outputs of the cerebellum being viewed as representations of particular intervals rather than pulses as implied by pacemaker models. It will be important in future studies to make direct comparisons between patients with cerebellar and basal ganglia dysfunction, seeking dissociations as have been observed in the current experiment. In this manner, a functional analysis can be established of the neural systems involved in temporal processing.

References

Aitkin, L., & Boyd, J. (1975). Responses of single units in cerebellar vermis of the cat to monaural and binaural stimuli. *Journal of Neurophysiology, 38,* 418–419.

Akshoomoff, N. A., & Courchesne, E. (1992). A new role for the cerebellum in cognitive operations. *Behavioral Neuroscience, 106,* 731–738.

Akshoomoff, N. A., Courchesne, E., Press, G. A., & Iragui, V. (1992). Contribution of the cerebellum to neuropsychological functioning: Evidence from a case of cerebellar degenerative disorder. *Neuropsychologia, 30,* 315–328.

Akshoomoff, N. A., Courchesne, E., & Townsend, J. (1997). Attention coordination and anticipatory control. *International Review of Neurobiology, 41,* 575–598.

Azizi, S. A., Burne, R. A., & Woodward, D. J. (1985). The auditory corticopontocerebellar projection in the rat: Inputs to the paraflocculus and midvermis. An anatomical and physiological study. *Experimental Brain Research, 59,* 36–49.

Benton, A. L., & Hamsher, K. (1978). *The Multilingual Aphasia Examination.* Iowa City: University of Iowa Press.

Braitenberg, V. (1967). Is the cerebellar cortex a biological clock in the millisecond range? *Progress in Brain Research, 25,* 334–346.

Brown, S. W. (1997). Attentional resources in timing: Interference effects in concurrent temporal and nontemporal working memory tasks. *Perception and Psychophysics, 59,* 1118–1140.

Bruder, G. E., Towey, J., Friedman, D., Erhan, H., Jasiukaitis, P., & Tenke, C. (1992). Lateral asymmetries of event-related potential slow waves. *Journal of Psychophysiology, 6,* 97–110.

Buonomano, D., & Mauk, M. (1994). Neural network model of the cerebellum: Temporal discrimination and the timing of motor responses. *Neural Computation, 6,* 38–55.

Casini, L., & Macar, F. (1996a). Can the level of brain activity provide an index of the temporal performance? *Neuroscience Letters, 219,* 71–74.

Casini, L., & Macar, F. (1996b). Prefrontal slow potentials in temporal compared to nontemporal tasks. *Journal of Psychophysiology, 10,* 252–264.

Casini, L., & Macar, F. (1997). Effects of attention manipulation on perceived duration and intensity in the visual modality. *Memory and Cognition, 25,* 812–818.

Church, R. M. (1984). Properties of the internal clock. In J. Gibbon & L. Allan (Eds.), *Timing and time perception, Vol. 423* (pp. 566–582). New York: Annals of New York Academy of Sciences.

Corbetta, M., Miezin, F. M., Dobmeyer, S., Shulman, G. L., & Petersen, S. E. (1991). Selective and divided attention during visual discriminations of shape, color and speed: Functional anatomy by positron emission tomography. *Journal of Neuroscience, 11,* 2383–2402.

Courchesne, E., Townsend, J., Akshoomoff, N. A., Saitoh, O., Yeung-Courchesne, R., Lincoln, A., James, H., Haas, R. H., Schriebman, L., & Lau, L. (1994). Impairment in shifting attention in autistic and cerebellar patients. *Behavioral Neuroscience, 108,* 848–865.

Daum, I., Ackermann, H., Schugens, M. M., Reimold, C., Dichgans, J., & Birbaumer, N. (1993a). The cerebellum and cognitive functions in humans. *Behavioral Neuroscience, 107,* 411–419.

Daum, I., Schugens, M. M., Ackermann, H., Lutzenberger, W., Dichgans, J., & Birbaumer, N. (1993b). Classical conditioning after cerebellar lesions in humans. *Behavioral Neuroscience, 107,* 748–756.

Elbert, T., Ulrich, R., Rockstroh, B., & Lutzenberger, W. (1991). The processing of temporal intervals reflected by CNV-like brain potentials. *Psychophysiology, 28,* 648–655.

Fahle, M., & Braitenberg, V. (1984). Some quantitative aspects of cerebellar anatomy as a guide to speculation on cerebellar functions. In J. Bloedel, J. Dichgans, & W. Precht (Eds.), *Cerebellar functions* (pp. 186–200). Berlin, Germany: Springer-Verlag.

Fiala, J. C., Grossberg, S., & Bullock, D. (1996). Metabotropic glutamate receptor activation in cerebellar Purkinje cells as substrate for adaptive timing of the classically conditioned eye-blink response. *Journal of Neuroscience, 16,* 3760–3774.

Franz, E. A., Ivry, R., & Helmuth, L. (1996). Reduced timing variability in patients with unilateral cerebellar lesions during bimanual movements. *Journal of Cognitive Neuroscience, 8,* 107–118.

Fuster, J. M. (1981). The neurophysiology of prefrontal lobe. In V. B. Brooks (Ed.), *Handbook of physiology: Nervous system, motor control* (pp. 1149–1178). Bethesda, MD: American Physiology Society.

Gibbon, J., Church, R. M., & Meck, W. H. (1984). Scalar timing in memory. In J. Gibbon & L. Allan (Eds.), *Timing and time perception, Vol. 423* (pp. 52–77). New York: Annals of New York Academy of Sciences.

Gibbon, J., Malapani, C., Dale, C. L., & Gallistel, C. R. (1997). Toward a neurobiology of temporal cognition: Advances and challenges. *Current Opinion in Neurobiology, 7,* 170–184.

Goldman-Rakic, P. S. (1992). Working memory and the mind. *Scientific American, 267,* 111–117.

Grant, D., & Berg, E. A. (1948). A behavioral analysis of degree of reinforcement and ease of shifting to new responses in a Weigl-type card sorting problem. *Journal of Experimental Psychology, 38,* 404–411.

Grill, S. E., Hallett, M., Marcus, C., & McShane, L. (1994). Disturbances of kinaesthesia in patients with cerebellar disorders. *Brain, 117,* 1433–1447.

Helmuth, L., Ivry, R., & Shimizu, N. (1997). Preserved performance by cerebellar patients on tests of word generation, discrimination learning, and attention. *Learning & Memory, 3,* 456–474.

Hore, J., Wild, B., & Diener, H. C. (1991). Cerebellar dysmetria at the elbow, wrist, and fingers. *Journal of Neurophysiology, 65,* 563–571.

Huffman, R. F., & Henson, O. W. (1990). The descending auditory pathway and acousticomotor systems: Connections with the inferior colliculus. *Brain Research Reviews, 15,* 295–323.

Ivry, R. (1993). Cerebellar involvement in the explicit representation of temporal information. In P. Tallal, A. Galaburda, R. R. Llinas, & C. Von Euler (Eds.), *Temporal information processing in the nervous system: Special reference to dyslexia and dysphasia, Vol. 682* (pp. 214–230). New York: Annals of New York Academy of Sciences.

Ivry, R. (1996). The representation of temporal information in perception and motor control. *Current Opinion in Neurobiology, 6,* 851–857.

Ivry, R., & Diener, H. C. (1991). Impaired velocity perception in patients with lesions of the cerebellum. *Journal of Cognitive Neuroscience, 3,* 355–366.

Ivry, R., & Hazeltine, R. E. (1995). The perception and production of temporal intervals across a range of durations: Evidence for a common timing mechanism. *Journal of Experimental Psychology: Human Perception and Performance, 21,* 1–12.

Ivry, R., & Keele, S. (1989). Timing functions of the cerebellum. *Journal of Cognitive Neuroscience, 1,* 136–152.

Ivry, R., Keele, S., & Diener, H. C. (1988). Dissociation of the lateral and medial cerebellum in movement timing and movement execution. *Experimental Brain Research, 73,* 167–180.

Jueptner, M., Flerlch, L., Weiller, C., Mueller, S., & Diener, H. C. (1996). The human cerebellum and temporal information processing—results from a PET experiment. *Neuroreport, 7,* 2761–2765.

Jueptner, M., Rijntjes, M., Weiller, C., Faiss, J. H., Timman, D., Mueller, S., & Diener, H. C. (1995). Localization of a cerebellar timing process using PET. *Neurology, 45,* 1540–1545.

Knight, R. T. (1994). Attention regulation and human prefrontal cortex. In A. M. Thierry, J. Glowinski, P. Goldman-Rakic, & Y. Christen (Eds.), *Motor and cognitive functions of the prefrontal cortex* (pp. 160–173). Berlin, Germany: Springer-Verlag.

Macar, F., Grondin, S., & Casini, L. (1994). Controlled attention-sharing influences time estimation. *Memory and Cognition, 22,* 673–686.

Madigan, R., & Williams, D. (1987). Maximum-likelihood procedures in two-alternative forced-choice: Evaluation and recommendations. *Perception & Psychophysics, 28,* 240–249.

Mangels, J. A. (1997). Strategic processing and memory for temporal order in patients with frontal lobe lesions. *Neuropsychology, 11,* 207–221.

Mangels, J. A., Ivry, R., & Shimizu, N. (1998). Dissociable contributions of the prefrontal and neocerebellar cortex to time perception. *Cognitive Brain Research, 7,* 15–39.

Maquet, P., Lejeune, H., Pouthas, V., Bonnet, M., Casini, L., Macar, F., Timsit-Berthier, M., Vidal, F., Ferrara, A., Degueldre, C., Quaglia, L., Delfiore, G., Luxen, A., Woods, R., Mazziotta, J. C., & Comar, D. (1996). Brain activation induced by estimation of duration. A PET study. *NeuroImage, 3,* 119–126.

Meck, W. H. (1996). Neuropharmacology of timing and time perception. *Cognitive Brain Research, 3,* 227–242.

Middleton, F. A., & Strick, P. L. (1994). Anatomical evidence for cerebellar and basal ganglia involvement in higher cognitive function. *Science, 266,* 458–461.

Milner, B., Corsi, P., & Leonard, G. (1991). Frontal-lobe contribution to recency judgments. *Neuropsychologia, 29,* 601–618.

Nawrot, M., & Rizzo, M. (1995). Motion perception deficits from midline cerebellar lesions in human. *Vision Research, 35,* 723–731.

Nichelli, P., Clark, K., Hollnagel, C., & Grafman, J. (1995). Duration processing after frontal lobe lesions. In J. Grafman, K. J. Holyoak, & F. Boller (Eds.), *Structure and functions of the human prefrontal cortex, Vol. 769* (pp. 183–190). New York: Annals of the New York Academy of Sciences.

Olton, D. S., Wenk, G. L., Church, R. M., & Meck, W. H. (1988). Attention and the frontal cortex as examined by simultaneous temporal processing. *Neuropsychologia, 26,* 307–318.

Pandya, D. N., & Seltzer, B. (1982). Association areas of the cerebral cortex. *TINS, 5,* 386–390.

Pentland, A. (1980). Maximum likelihood estimation: The best PEST. *Perception & Psychophysics, 28,* 377–379.

Perret, S., Ruiz, B., & Mauk, M. (1993). Cerebellar cortex lesions disrupt learning-dependent timing of conditioned eyelid responses. *Journal of Neuroscience, 13,* 1708–1718.

Ravizza, S. M., & Ivry, R. B. (1998). *Comparison of the cerebellum and basal ganglia in shifting attention.* Paper presented at the 5th Annual Meeting of the Cognitive Neuroscience Society, San Francisco, CA.

Shimamura, A. P. (1995). Memory and frontal lobe function. In M. S. Gazzaniga (Ed.), *The cognitive neuroscience* (pp. 803–813). Cambridge, MA: MIT Press.

Shimamura, A. P., Janowsky, J. S., & Squire, L. R. (1990). Memory for the temporal order of events in patients with frontal lobe lesions and amnesic patients. *Neuropsychologia, 28,* 803–813.

Steinmetz, J., Logan, C., Rosen, D., Thompson, J., Lavond, D., & Thompson, R. (1987). Initial localization of the acoustic conditioned stimulus projection system to the cerebellum essential for classical eyelid conditioning. *Proceedings of the National Academy of Sciences USA, 84,* 3531–3535.

Stuss, D. T., & Benson, D. F. (1984). Neuropsychological studies of the frontal lobes. *Psychological Bulletin, 95,* 3–28.

Taylor, M., & Creelman, C. (1967). PEST: Efficient estimates of probability functions. *Journal of the Acoustic Society of America, 41,* 782–787.

Thompson, R. (1990). Neural mechanisms of classical conditioning in mammals. *Philosophical Transactions of the Royal Society (Section B), 329,* 161–170.

Treisman, M. (1963). Temporal discrimination and the indifference interval: Implications for a model of the "internal clock." *Psychological Monographs, 77,* 1–31.

Von Steinbuchel, N., Wittman, M., & Poeppel, E. (1996). Timing in perceptual and motor tasks after disturbances of the brain. In M. A. Pastor & J. Artieda (Eds.), *Time, internal clocks and movement, Vol. 115* (pp. 281–304). Amsterdam: Elsevier Science.

Wechsler, D. (1987). *Wechsler Adult Intelligence Scale—Revised.* San Antonio, TX: The Psychological Corporation.

Woodruff-Pak, D. S., Papka, M., & Ivry, R. (1996). Cerebellar involvement in eyeblink classical conditioning in humans. *Neuropsychology, 10,* 443–458.

Zakay, D. (1989). Subjective and attentional resource allocation: An integrated model of time estimation. In I. Levin & D. Zakay (Eds.), *Time and human cognition, Vol. 59* (pp. 365–397). Amsterdam: Elsevier Science.

Received December 1, 1997
Revision received June 19, 1998
Accepted June 22, 1998 ■

New Editors Appointed, 2000-2005

The Publications and Communications Board of the American Psychological Association announces the appointment of three new editors for 6-year terms beginning in 2000.

As of January 1, 1999, manuscripts should be directed as follows:

- For **Experimental and Clinical Psychopharmacology**, submit manuscripts to Warren K. Bickel, PhD, Department of Psychiatry, University of Vermont, 38 Fletcher Place, Burlington, VT 05401-1419.

- For the **Journal of Counseling Psychology**, submit manuscripts to Jo-Ida C. Hansen, PhD, Department of Psychology, University of Minnesota, 75 East River Road, Minneapolis, MN 55455-0344.

- For the **Journal of Experimental Psychology: Human Perception and Performance**, submit manuscripts to David A. Rosenbaum, PhD, Department of Psychology, Pennsylvania State University, 642 Moore Building, University Park, PA 16802-3104.

Manuscript submission patterns make the precise date of completion of the 1999 volumes uncertain. Current editors, Charles R. Schuster, PhD; Clara E. Hill, PhD; and Thomas H. Carr, PhD, respectively, will receive and consider manuscripts through December 31, 1998. Should 1999 volumes be completed before that date, manuscripts will be redirected to the new editors for consideration in 2000 volumes.