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Cerebellar Damage Impairs Automaticity of a Recently Practiced Movement

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Lang, Catherine E. and Amy J. Bastian. Cerebellar damage impairs automaticity of a recently practiced movement. *J Neurophysiol* 87: 1336–1347, 2002; 10.1152/jn.00368.2001. It has been suggested that the cerebellum plays a critical role in learning to make movements more “automatic” (i.e., requiring less attention to the details of a movement). We hypothesized that cerebellar damage compromises learning of movement automaticity, resulting in increased attentional demands for movement control. The purpose of our study was to determine whether cerebellar damage disrupts the ability to make a practiced movement more automatic. We developed a dual task paradigm using two tasks that did not have overlapping sensory or motor requirements for execution. Our motor task required subjects to maintain an upright posture while performing a figure-8 movement using their arm. This motor task was chosen to simulate requirements of everyday movements (e.g., standing while reaching for objects), but it was novel enough to require practice for improvement. Our secondary task was an auditory vigilance task where subjects listened to letter sequences and were asked to identify the number of times a target letter was heard. We tested controls and people with cerebellar damage as they practiced the movement task alone and then performed it with the auditory task. We recorded 3D position data from the arm, trunk, and leg during the movement task. Errors were recorded for both the movement and the letter tasks. Our results show that cerebellar subjects can improve the movement to a very limited extent with practice. Unlike controls, the motor performance of cerebellar subjects deteriorates to prepractice levels when attention is focused away from the movement during dual task trials. Control subjects’ insensitivity to dual task interference after practice was due to learned movement automaticity and was not a reflection of better dual task performance generally. Overall, our findings suggest that the cerebellum may be important for shifting movement performance from an attentionally demanding (unpracticed) state to a more automatic (practiced) state.

INTRODUCTION

The ability to successfully execute movements while attending to external stimuli is a critical component of human behavior. Many movements are performed without attention being explicitly directed toward the details of the movement. This is particularly true for movements that require low precision or for movements that are commonly made (Bernstein 1967). For example, when operating a car, an experienced driver does not explicitly focus on the details of the movement required to hit the brake. Instead, the driver may be focused on the color of the

traffic light or the presence of another car. Movements such as these may be considered relatively automatic in the sense that they do not require attention to the implementation of the movement.

Several people have speculated that the cerebellum may be important in the acquisition and/or execution of more automatic movements (Eccles et al. 1967; Holmes 1939; Thach 1998; Thach et al. 1992). Support for this idea comes from human studies showing that cerebellar damage can impair learning of several motor tasks including visuomotor adaptation to prisms (Martin et al. 1996; Weiner et al. 1983), adaptation of anticipatory muscle activity during catching (Lang and Bastian 1999, 2001), learning a sequence of key presses (Doyon et al. 1997; Molinari et al. 1997), and adaptation of the gain of ballistic arm movements (Deuschl et al. 1996). The idea that the cerebellum is important in more automatic movements is consistent with the descriptions of movement deficits given by cerebellar patients. A telling quote from a cerebellar patient of Gordon Holmes (Holmes 1939) reads “The movements of my left arm are done subconsciously, but I have to think out each movement of the right (affected) arm.”

Neuroimaging studies indicate that the cerebellum may participate in different phases of motor learning (Doyon et al. 1996; Jenkins et al. 1994; Jueptner et al. 1997a,b; Shadmehr and Holcomb 1997; Toni et al. 1998; van Mier et al. 1998). It is unclear whether the cerebellum is most active in acquisition of the learned movement, execution of the movement once it has been learned, or both. In sequential key press tasks, cerebellar activity has been shown to be greatest during early learning and to decrease once the task was well practiced (Doyon et al. 1996; Jenkins et al. 1994; Jueptner et al. 1997b; Toni et al. 1998). A similar finding was reported when subjects learn to draw a maze: left lateral cerebellar cortex activity was greatest during unpracticed performance and decreased as the movement became more skilled (van Mier et al. 1998). In contrast, Shadmehr and Holcomb (1997) showed that cerebellar activity increased only when a practiced movement was performed at a later time. In that study, subjects learned to make arm movements in a velocity-dependent force field, which may be a more difficult and novel task compared with the other studies.

Other neuroimaging studies have looked for brain regions

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involved in directing attention toward or away from a movement (Grafton et al. 1995; Hazeltine et al. 1997; Honda et al. 1998; Jueptner et al. 1997a). Dorsal prefrontal cortex was the area most consistently activated when subjects were explicitly focused on learning a sequence of key presses (Grafton et al. 1995; Hazeltine et al. 1997; Honda et al. 1998) or when subjects attended to a previously learned sequence (Jueptner et al. 1997a). In contrast, more traditional motor areas (primary motor cortex, supplementary motor area, premotor cortex, and subcortical motor areas) were more important when learning a movement implicitly (Grafton et al. 1995; Hazeltine et al. 1997; Honda et al. 1998). These findings suggest that different brain areas are involved in learning to make movements with or without attention directed toward the movement.

One interesting study has looked at the automatization of a visuomotor sequence in people with CNS damage (Doyon et al. 1998). People with cerebellar damage or Parkinson's disease showed interference between a visuospatial memory task and performance of a previously practiced sequence of key presses (Doyon et al. 1998). During dual task trials, subjects showed degradation in performance of the visuospatial memory task but not the sequential movement task. Doyon and colleagues' results show that cerebellar subjects are impaired in performing two tasks with visuospatial requirements simultaneously. We sought to determine whether cerebellar subjects have a more general deficit in dual task performance that reflects a failure of learning movement automaticity.

The purpose of our study was to determine whether cerebellar damage disrupts the ability to make a practiced movement more automatic. We developed a dual task paradigm using two tasks that did not have overlapping sensory or motor requirements for task execution. Our motor task required subjects to maintain an upright posture while performing a figure-8 movement using their arm. This motor task was chosen to simulate requirements of every day movements (e.g., standing while reaching for objects), but it was novel enough to require practice for improvement. Our secondary task was an auditory vigilance task where subjects listened to letter sequences and were asked to identify the number of times a target letter was heard. We tested controls and people with cerebellar damage as they practiced the movement task alone and then performed it with the auditory task. Our results show that

cerebellar subjects can improve the movement to a very limited extent with practice. Unlike controls, the motor performance of cerebellar subjects deteriorates to prepractice levels when attention is focused away from the movement during dual task trials. This suggests that the cerebellum may be important for shifting movement performance from an attentionally demanding (unpracticed) state to a more automatic (practiced) state.

METHODS

Subjects

Ten subjects with cerebellar damage (Table 1) and 10 control subjects participated in *experiment 1*. Cerebellar damage was confirmed by computed tomography or magnetic resonance imaging. When available, results of genetic testing were used to confirm specific forms of cerebellar atrophy. All cerebellar subjects underwent a clinical neurological examination to determine the severity of the movement deficit and to check for signs of involvement of other motor structures. Potential cerebellar subjects with involvement of other motor structures were excluded from participation. The cerebellar subjects tested in this study presented with limb ataxia, consisting of irregular arm and leg movements (by finger-nose-finger, Fisher, and heel-knee-shin tests) and truncal ataxia (by changes in stance and gait under various conditions). Clinical signs and task behavior were not systematically different in subjects with cerebellar atrophy versus those with an acute lesion. As in other lesion studies, the cerebellar subjects had incomplete lesions and thus presumably maintained some residual cerebellar function. Subject CBL-01 had extensive vermal damage due to surgical resection of an astrocytoma. CBL-01 exhibited nystagmus and had facial nerve involvement, but was not hyperreflexive and did not show a Babinski's sign. Subject CBL-02 had inferior olive hypertrophy with palatal myoclonus. Cerebellar subjects were tested by making movements on the side ipsilateral to the cerebellar damage, or in subjects with bilateral damage, on the more impaired side. Healthy control subjects were matched by age (mean 57.1 ± 6.1 yr), gender, and handedness to the cerebellar subjects. Eight additional healthy control subjects (age range 24–60 yr) participated in *experiment 2*. Informed consent was obtained from all subjects prior to testing.

Paradigm

Subjects were tested by performing a novel movement task (figure-8 task) in isolation and then in conjunction with an auditory

TABLE 1. Subject information

Subject	Age	Gender	Lesion Type and Location	Length of Illness	Arm Ataxia	Stance/Gait Ataxia	Assistive Device Used for Gait
CBL-01	23	F	Vermal split with vermal damage (left > right) due to tumor removal	2 yrs.	Mild	Mild	None
CBL-02	68	M	Inferior olive hypertrophy	5 yrs.	Mild	Moderate	Cane
CBL-03	63	M	Vermal and right medial cerebellar tumor treated with radiation therapy	4 mos.	Mild	Mild	Cane
CBL-04	45	F	Pancerebellar cortical atrophy	12 yrs.	Mild	Moderate	Cane
CBL-05	84	M	OPCA	7 yrs.	Moderate	Moderate	Rolling walker
CBL-06*	71	F	SCA6	29 yrs.	Moderate	Severe	2 person assist
CBL-07	40	M	SCA6	7 yrs.	Mild	Mild	None
CBL-08	33	M	Bilateral superior cerebellar artery hemorrhages with right > left	3 mos.	Moderate	Moderate	Rolling walker
CBL-09*	71	M	SCA6	10 yrs.	Severe	Severe	Rolling walker + person to assist
CBL-10	61	M	OPCA	2 yrs.	Moderate	Moderate	Rolling walker

OPCA, olivopontocerebellar atrophy; SCA 6, spinocerebellar atrophy type 6. * CBL-06 and CBL-09 were unable to stand without support and were therefore tested sitting.

distraction task. The figure-8 task required maintenance of upright posture while making coordinated movements of the trunk and arm. Figure 1 illustrates the experimental set-up for the figure-8 task. Subjects stood with feet approximately shoulder-width apart and performed the figure-8 movement with the arm. Two cerebellar subjects (CBL-06, CBL-09) were unable to stand without assistance; these subjects and their age-matched controls (CNT-06, CNT-09) were tested while sitting without back/trunk support. Of the eight cerebellar subjects tested standing, one (CBL-10) required physical assistance to keep from falling during the testing session. All subjects made continuous figure-8 movements around two flexible barriers with a baton. The barriers were parallel to the floor and positioned vertically at mid-chest level and anteriorly at 110% of arm length (far barrier) and 60% of arm length (near barrier). These barrier positions required subjects to move both the arm and the trunk. Subjects held a baton oriented parallel to the barriers (perpendicular to their forearm) and wore a wrist brace to minimize wrist joint movement. Subjects began and ended the figure-8 movements at verbal “start” and “stop” signals, respectively. Subjects were instructed to “make as many figure-8s as you can” during the 8-s trial. All subjects were aware that their performance was being assessed by the number of figure-8s that they could complete. Every one to three trials, we provided encouragement and also feedback about whether number of figure-8s was changing. Subjects were not required to follow a template of the figure-8 pattern and were not provided with feedback on the shape or consistency of the figure-8 pattern.

Automaticity is frequently evaluated by having subjects perform an interference or distraction task simultaneously with the more automatic task (Neumann 1984; Passingham 1996). We used an auditory vigilance task (letter task) in this study. For the letter task, subjects listened to recordings of 14-letter sequences. Each 14-letter sequence consisted of a random series of the same four letters (A, G, M, and O). The sequence began with the word start, followed by 14 letters (at 1.75 Hz, 8-s duration), and then ended with the word stop. At the end of each 14-letter sequence, subjects were asked to identify the number of times a target letter was heard. The target letter was changed for each trial. The letter task required auditory attention and was simple enough that subjects of most age and education levels could be successful.

The purpose of *experiment 1* was to test if cerebellar subjects were impaired in their ability to perform the two tasks simultaneously, *after* they had a chance to practice. For *experiment 1*, subjects were given

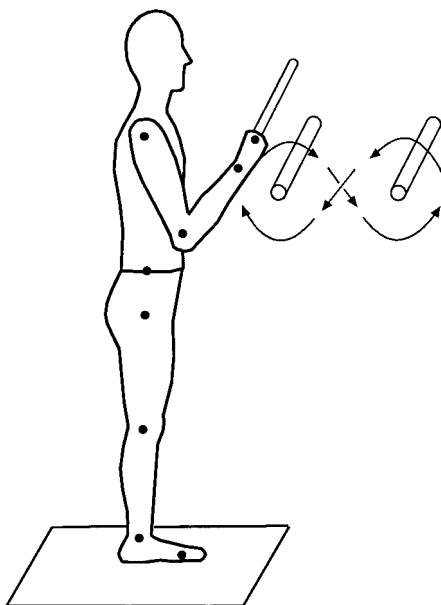


FIG. 1. Schematic of the figure-8 task.

one to three practice trials on the letter task to be sure that they understood the task. We recorded five baseline trials on the letter task alone. Then we recorded 20–25 trials of the figure-8 task alone. Finally we recorded five dual task trials. Cerebellar subjects were usually given more trials (higher end of the ranges listed above) to provide them with the most opportunity to be successful. When both tasks were performed simultaneously, subjects began the figure-8 task at the word start and ended at the word stop on the tape recording. During the dual task trials, subjects were instructed to try to be correct on the letter task; this was to ensure that attention was focused away from the movement.

The purpose of *experiment 2* was to test if the two tasks interfered with each other during practice in control subjects. For *experiment 2*, control subjects were instructed in the figure-8 task and the letter task without the opportunity to practice either task alone. We recorded 25–30 dual task trials. As in *experiment 1*, subjects in *experiment 2* were told to optimize performance on the letter task.

Data collection

Movements were recorded in 3D using infrared emitting markers placed on the subject's body (OPTOTRAK System, Northern Digital Inc., Waterloo, ON). Nine markers were placed on each subject as follows: 1) foot (fifth metatarsal head), 2) ankle (lateral malleolus), 3) knee (lateral joint line), 4) hip (greater trochanter), 5) pelvis (iliac crest), 6) shoulder (acromion process), 7) elbow (lateral epicondyle), 8) wrist (dorsal surface), and 9) hand (dorsal surface of third metacarpophalangeal joint). Two additional markers defined the location of the barriers. Marker position data were collected at 100 Hz. Additionally, an investigator recorded the number of target letters reported and the number of movement errors in each trial.

Data analysis

Position data were low-pass-filtered at 10 Hz. OPTOTRAK software was used to calculate marker positions, velocities, and joint angles. Custom software was used for the following analyses. The “start of movement” was defined as the time and position at which the wrist resultant velocity exceeded 50 mm/s. To ensure that we were comparing movement over the same amount of time for each subject, we analyzed the 6.5 s of data after the start of movement. This eliminated any effects due to delayed reaction times in cerebellar subjects.

For each letter task trial, the performance measure was the number of letter errors. An error on the letter task could be due an over- or underestimate of the number of times that the target letter was present in a given trial. For example, a score of two errors could be due to a subject over- or undercounting the number of target letters by two.

For each figure-8 task trial, the primary performance measures were the number of figure-8s completed and the number of movement errors. The number of figure-8s was determined by counting the successful figure-8 movements (baton passing outside the barriers in the appropriate “8” pattern) to the nearest 1/8th of a figure-8 (2 loops divided into quarters). The number of movement errors was determined by counting the occurrence of movement errors in each trial. A movement error occurred when the subject hit a barrier, failed to pass outside the barrier, made the figure-8 backwards, or made movements that were not figure-8s (e.g., circles).

We calculated two additional variables for each figure-8 trial: average hand speed and average figure-8 size. The average hand speed was calculated as the distance traveled by the hand divided by trial time. The average figure-8 size was calculated as the distance traveled by the hand during successful figure-8s divided by the number of figure-8s (in mm/figure-8).

Experiment 1 compared movement task performance *after practice* with dual task performance in cerebellar and control subjects. For *experiment 1*, we plotted each kinematic measure as a function of trial

for each subject. Means for the figure-8 task performance measures were computed for 1) the first three trials in the figure-8 task alone, 2) the last five trials in the figure-8 task alone, and 3) the five dual task trials. The mean number of letter errors was computed for the five baseline letter task trials and the five dual task trials. Means were compared between groups (cerebellar versus control) and phases (early versus late versus dual task) using repeated measures analyses of variance (ANOVAs).

Additionally, we determined the percentage change in the number of figure-8s, average figure-8 speed, and average figure-8 size between the movement task and the dual task. Percentage change was calculated by

$$\text{Percent Change} = (\text{Mean}_{\text{dual task trials}} - \text{Mean}_{\text{last 5 movement trials}}) \div \text{Mean}_{\text{last 5 movement trials}} \times 100$$

Negative percentage change values reflect fewer figure-8s completed, slower average hand speeds, and smaller average figure-8 sizes. Percentage change was compared between groups using *t*-tests. Statistical analyses were done with Statistica software (StatSoft, Tulsa, OK) and the criterion level for statistical significance was set at $P < 0.05$. Scheffé post hoc testing was performed when significant main or interaction effects were found.

Experiment 2 tested dual task performance during practice in control subjects only. We compared the rate of learning of eight control subjects practicing the figure-8 task alone (from *experiment 1*) with the rate of learning of eight additional control subjects practicing both tasks simultaneously (from *experiment 2*). To do this, we modeled the improvement (trial-by-trial changes) in the number of figure-8s in *experiment 1* and in *experiment 2* using an exponential decay function. The decay constant from the exponential function has been used as a measure of the rate of adaptation (Deuschl et al. 1996; Lang and Bastian 1999; Martin et al. 1996). In this analysis, the decay constant was used as our rate of learning and represents the number of trials for a subject to proceed approximately two-thirds of the way through the learning process. Rates of learning were compared between control groups (*experiment 1*, single task practice versus *experiment 2*, dual task practice) using a *t*-test. We also used repeated measures ANOVA to determine if initial and final performance under the two practice conditions differed. Specifically, we compared the means of the first three trials and the last five trials of each measure (number of figure-8s, number of movement errors, number of letter errors, average hand speed, and average figure-8 size). The two control subjects who were tested during sitting in *experiment 1* were not included in this analysis (CNT-06 and CNT-09).

RESULTS

Experiment 1: distraction after practice

Control and cerebellar groups did not differ in performance on the baseline letter task ($P = 0.400$). Subjects in both groups typically had no errors, or a single error, during one of the five baseline trials. Overall, both groups made an average of less than one error per letter task trial (cerebellar group 0.4 ± 0.19 ; control group 0.22 ± 0.09).

Control subjects performed better than the cerebellar subjects on the figure-8 task, alone and during the dual task condition. Figure 2 shows hand paths from selected single trials for a control and two cerebellar subjects. For each subject, we show the first trial of the figure-8 task alone, the last trial of the figure-8 task alone, and a dual task trial. The number of movement errors for each trial is given in the bottom right corner of each trace. The control subject (Fig. 2A, CNT-07) completed many more figure-8s during the last trial than the first trial. The control subject had the same consistent hand

path in the dual task trial as in the last figure-8 trial and made no movement errors on these three trials. The two cerebellar subjects in Fig. 2 completed slightly more figure-8s on the last trial than the first trial of the figure-8 task alone (compare first and second columns). During the dual task trial, cerebellar subjects performed poorly. CBL-01 (Fig. 2B) moved slightly slower, had an irregular hand path, and missed the barrier two times. CBL-07 (Fig. 2C) continued to move at the same speed but made many more movement errors than the last figure-8 trial. He failed to move outside the barriers on two of the loops and hit the barriers three times in this dual task trial.

Figure 3 shows trial-by-trial plots of the number of figure-8s and average hand speed, as well as movement and letter errors. Plots are from the same subjects shown in Fig. 1. CNT-07 (Fig. 3A) increased the number of figure-8s and hand speed with practice and showed minimal degradation of performance during the dual task trials. The percentage change from late figure-8 trials to dual task trials was -0.7% for the number of figure-8s and 2.1% for the average hand speed. In both the single and the dual task trials, CNT-07 made few movement errors and no letter errors.

Cerebellar subjects performed fewer figure-8s at slower hand speeds, showed modest to minimal improvement with practice, and had degraded performance during dual task trials. In Fig. 3, CBL-01 showed some improvement in the number of figure-8s and hand speed with practice. She completed fewer figure-8s during dual task trials than late figure-8 trials (-59.5%) and reduced her hand speed slightly (-8.7%). CBL-07 (Fig. 3C) showed some improvement in the number of figure-8s and hand speed with practice, but completed fewer figure-8s in the dual task trials than the late figure-8 task trials (-42.3%). Note that on the second and third dual task trials, CBL-07 made as many figure-8s as he had after practice, but made several errors on those two trials. Overall, CBL-07 did not change his average speed much (7.7%), but made more than twice the number of movement errors in the dual task trials.

Table 2 shows the number of figure-8s for all subjects. Values listed are means of the first three figure-8 task trials, the last five figure-8 task trials, the five dual task trials, and then the percent change due to the dual task condition. The cerebellar subjects typically completed fewer figure-8s than controls. Only the cerebellar group showed a decrease in the number of figure-8s in the dual task trials ($-27.9 \pm 6.4\%$ for the cerebellar group versus $1.6 \pm 3.0\%$ for the control group, $P = 0.001$). In fact, Table 2 shows that the cerebellar group decreased their performance to prepractice (early) levels during the dual task trials. This decrease was due in large to the occurrence of movement errors. Table 3 shows the average hand speed of all subjects for the last five figure-8 task trials and the dual task trials. The cerebellar group moved more slowly than controls. Cerebellar subjects showed a mean percentage change in average hand speed of $-6.6 \pm 4.0\%$ compared with $5.2 \pm 4.8\%$ for the control group. These values approached but were not statistically different from each other ($P = 0.075$).

Figure 4 shows group data for the number of figure-8s and the movement and letter errors. The control group completed more figure-8s per trial than the cerebellar group (group main effect, $P < 0.001$). The control group (Fig. 4A) increased the number of figure-8s they could perform after they practiced the

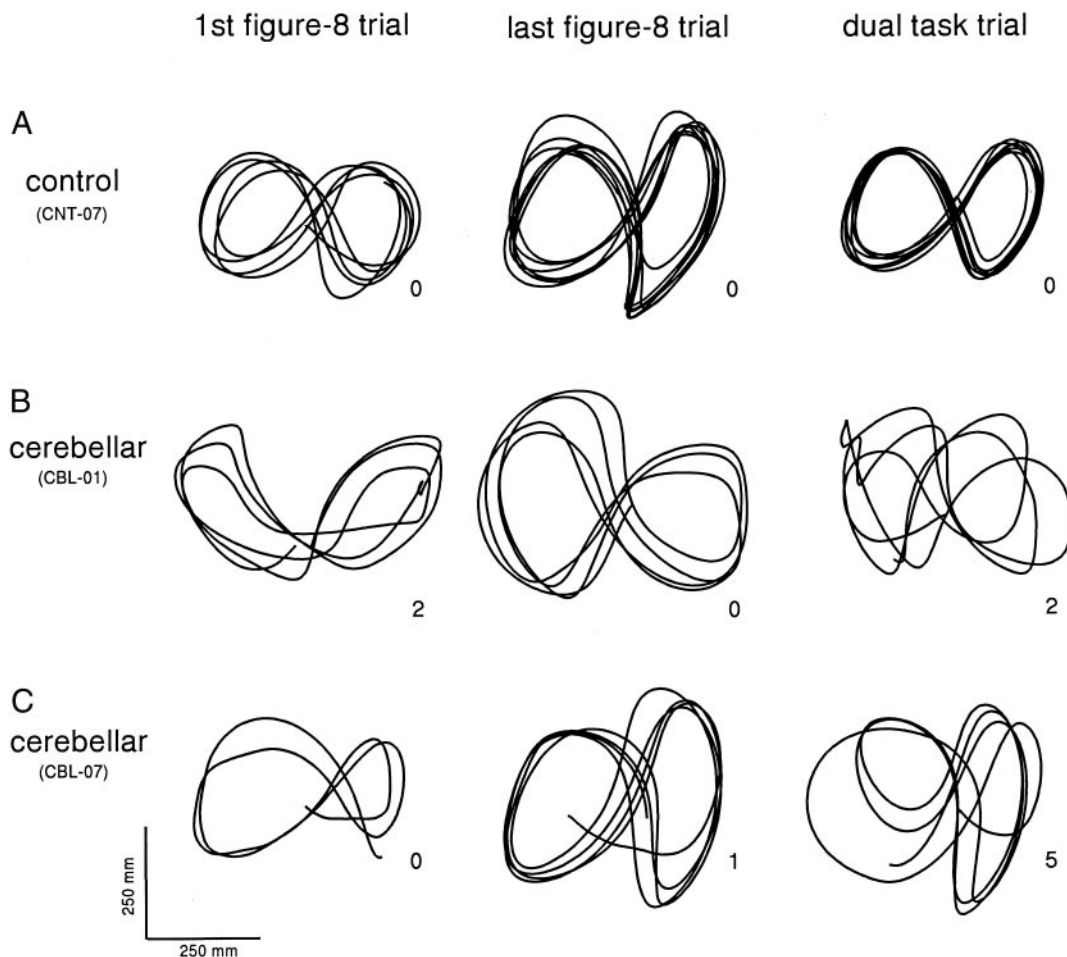


FIG. 2. Sample hand paths from selected trials in a control subject (A) and 2 cerebellar subjects (B and C) from *experiment 1*. Hand paths from the first figure-8 task trial, the last figure-8 task trial, and a dual task trial are shown for each subject. The number of movement errors for the trial is given in the bottom right corner of each trace.

figure-8 task ($P = 0.001$). They performed the same number of figure-8s in the dual task trials as in the late figure-8 task trials ($P = 0.905$). The cerebellar group (Fig. 4B) increased the number of figure-8s after they practiced the figure-8 task ($P = 0.002$), although to a much lesser extent than controls. The cerebellar group showed a marked decrease in the number of figure-8s during the dual task trials than the late figure-8 task trials ($P = 0.002$). This was highly significant, regardless of whether we tested the absolute change or percentage change in figure-8s.

The control group had the same number of movement errors in the dual task trials as in the late figure-8 task trials ($P = 0.689$). The cerebellar group made more movement errors in the dual task trials than the early and late figure-8 task trials ($P = 0.012$). For both groups, the number of letter errors were similar and did not change from single to dual task trials ($P = 0.999$). This is due to the fact that subjects were instructed to optimize performance on the letter task during the dual task trials.

We wondered whether poor cerebellar movement performance on dual task trials was due, in part, to larger figure-8 hand paths and/or deficits in trunk control. Analysis of the hand paths showed that both groups decreased the average figure-8 size with practice ($P = 0.023$). The control group averaged 1534 ± 71 mm/figure-8 in the early figure-8 task trials and

1411 ± 110 mm/figure-8 in the late figure-8 trials. The cerebellar group averaged 1700 ± 78 mm/figure-8 in the early figure-8 task trials and 1546 ± 84 mm/figure-8 in the late figure-8 trials. Table 3 shows that figure-8 size did not change during the dual task trials in either group ($P = 0.938$). Thus the change in the number of figure-8s with distraction was not due to an increase in hand path length. We also found that neither the control nor the cerebellar group changed the extent of trunk excursion during dual task trials. Figure 5 shows elbow, shoulder, and trunk angles changing over time for a control and cerebellar subject moving in the single and dual task conditions. During the figure-8 task alone (Fig. 5, A and C), the cerebellar subject (CBL-02) moved slower than the control and showed a different pattern of joint movement, particularly in the shoulder and trunk. During the dual task condition (Fig. 5, B and D), neither subject increased the range of motion in the arm joints or trunk. This cerebellar subject showed a slight reduction in trunk movement when performing dual tasks, though this was not a consistent finding across either group. Note that the cerebellar subject erroneously made an extra circle around the far barrier in the middle of the trial, accounting for the change in angular movement for 2.5–5.0 s (Fig. 5D). Overall, the increased irregularity of cerebellar movement during distraction was typically due to a spatial error in the

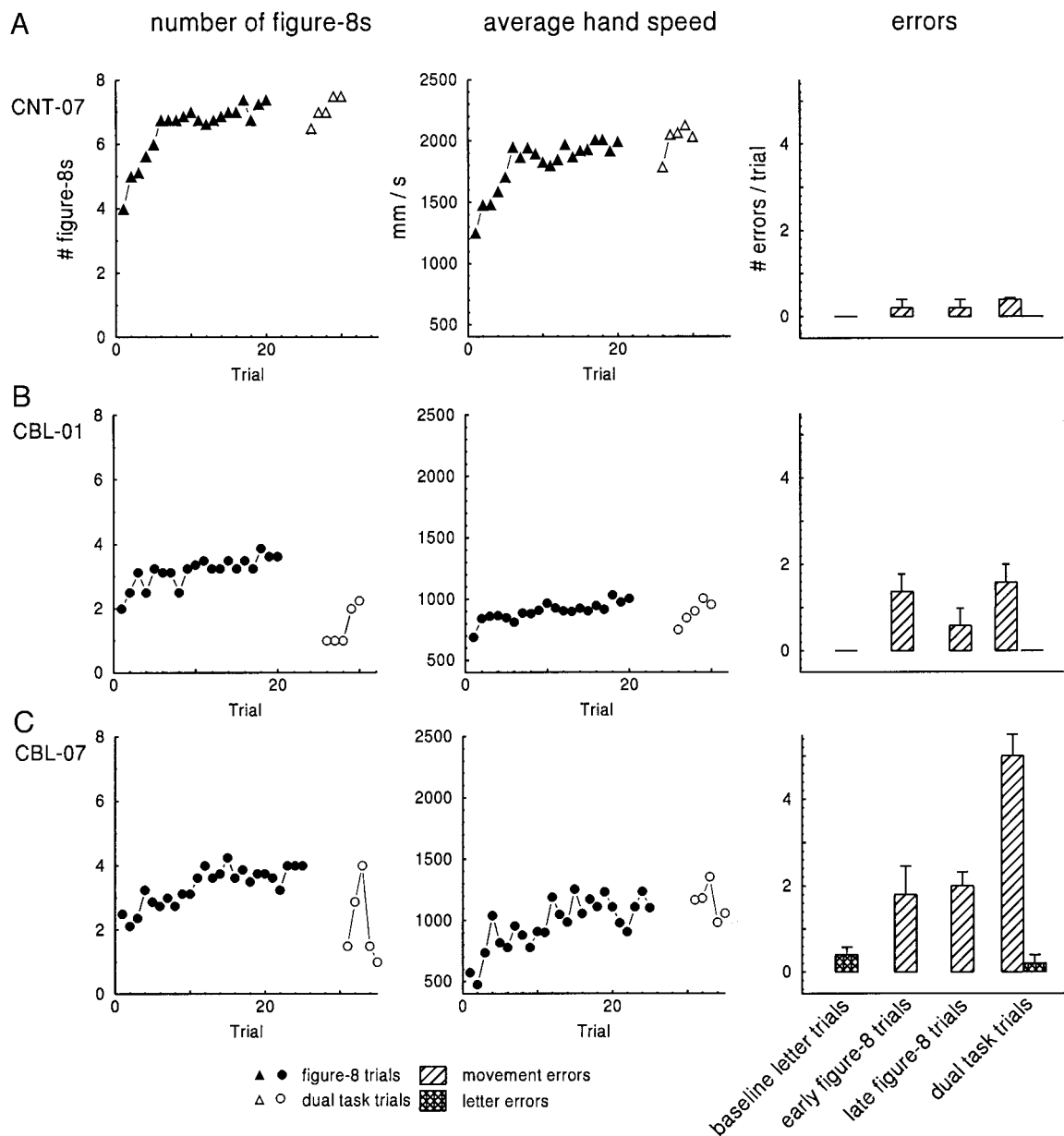


FIG. 3. Plots of the number of figure-8s, average hand speed, and movement and letter errors for a control (A) and 2 cerebellar subjects (B and C) from *experiment 1*. Data are from the same subjects shown in Fig. 2. Control data are represented by triangles. Cerebellar data are represented by circles. Closed symbols indicate figure-8 trials alone. Open symbols indicate dual task trials. Movement (striped bars) and letter errors (hatched bars) are averaged (+SE) in 5 trial blocks where “early” is the average of the first 5 trials and “late” is the average of the last 5 trials.

figure-8 movement (e.g., wrong direction or barrier contact) and not due to excessive movement at a given joint.

Does poor movement performance explain degraded dual task performance?

We wondered whether the interference during dual task trials was due to the general difficulty cerebellar subjects had performing the figure-8 task. Stated simply, if a subject is bad at a movement, then dividing attention with a secondary task may be more devastating than if a subject is good at a movement. Inspection of individual data (Table 2) suggests that this does not account for the degradation of cerebellar performance in the dual task trials. For example, CBL-10 can complete

slightly more figure-8s (5.08, Late column in Table 2) after practice than CNT-03 and CNT-05 (4.85 and 4.53 figure-8s, respectively). However, CBL-10 decreases the number of figure-8s he completes in the dual task condition (3.90, Dual task column in Table 2). CNT-03 and CNT-05 do not show this degradation during dual task trials (5.33 and 5.1 figure-8s, respectively). We also looked for relationships between initial task performance and dual task performance. A linear regression showed that initial task performance could account for slightly less than one-third of the variance in dual task performance degradation as measured by the absolute change in figure-8s (Early column versus difference between Late and Dual columns, $R^2 = 0.210$) or percentage change in figure-8s

TABLE 2. Number of figure-8s before practice, after practice, and during dual task performance

Subject	Number of Figure-8s				Subject	Number of Figure-8s			
	Early	Late	Dual task	Change (%)		Early	Late	Dual task	Change (%)
CBL-01	2.54	3.58	1.45	-59.5	CNT-01	7.21	7.95	8.08	1.6
CBL-02	2.67	2.85	1.05	-63.2	CNT-02	3.58	7.55	7.15	-5.3
CBL-03	3.46	3.15	2.83	-10.2	CNT-03	4.08	4.85	5.33	9.9
CBL-04	2.88	3.68	3.18	-13.6	CNT-04	4.42	7.03	6.70	-4.7
CBL-05	2.13	3.43	2.90	-15.5	CNT-05	4.17	4.53	5.1	12.6
CBL-06	2.29	2.85	2.70	-5.3	CNT-06	4.29	5.33	5.65	6.0
CBL-07	2.33	3.78	2.18	-42.3	CNT-07	4.71	7.15	7.10	-0.7
CBL-08	1.17	1.90	1.38	-27.6	CNT-08	5.88	7.15	8.1	13.3
CBL-09	2.17	2.68	2.18	-18.7	CNT-09	3.63	5.58	5.65	1.3
CBL-10	3.54	5.08	3.90	-23.2	CNT-10	5.13	8.33	6.85	-17.8
Mean ± SE	2.5 ± 0.2	3.3 ± 0.3	2.4 ± 0.3	-27.9 ± 6.4	Mean ± SE	4.7 ± 0.4	6.5 ± 0.4	6.6 ± 0.3	1.6 ± 3.0

Early, mean first 3 trials; late, mean last five figure-8 task trials; dual task, mean of five dual task trials; change, percentage change from late to dual task.

(Early column versus Change column, $R^2 = 0.321$). When late task performance was added as a factor to the regression equation, it did not account for any additional variance in dual task performance degradation.

To further test whether cerebellar dual task interference could be explained by poor motor performance, we studied three of the cerebellar subjects performing an easier version of the movement task. In this variation, we had CBL-01, CBL-07, and CBL-08 make a circle around the barriers instead of figure-8s, i.e., we reduced the spatial complexity of the task. We assessed their performance by counting the number of circles (to the nearest one-eighth) they completed and counting the number of movement errors they made. Results from this variation are shown in Table 4. Despite the improved motor performance on this easier task, these three cerebellar subjects show a decrease in the number of circles and an increase in movement errors during dual task trials. In fact, these subjects drop back down to their early (prepractice) level of movement performance when they had to perform dual tasks.

Experiment 2: distraction during practice for control subjects

The purpose of *experiment 2* was to test whether the two tasks interfered with each other *during* practice (i.e., early in the learning process) in control subjects. This allowed us to determine whether the noninterference observed in practiced

controls was really due to learned movement automaticity or simply due to better performance of dual tasks. For *experiment 2*, controls were tested while performing dual task trials without prior experience of either task. We compared the rate of learning during dual task practice (*experiment 2*) with the rate of learning during single task practice (from control subjects in *experiment 1*). Figure 6A shows data from a single subject (CNT-04) practicing the figure-8 task alone; she had a learning rate (decay constant) of 3.0 trials. In comparison, Fig. 6B shows data from another single subject (CNT-18) practicing under dual task conditions; he had a learning rate of 9.7 trials. Figure 6, C and D, show group data for *experiment 1* (controls) versus *experiment 2*. The group that practiced under dual task conditions learned at a slower rate (*experiment 2* = 7.9 ± 1.2 trials) than the group that practiced the figure-8 task alone (*experiment 1* = 3.3 ± 0.5 trials, $P = 0.004$). Rates of learning and asymptotes for individual control subjects in *experiment 1* and *experiment 2* are given in Table 5. Asymptotes (modeled level at which performance reached a plateau) were not different between the two groups ($P = 0.296$). Likewise, final performance measures (number of figure-8s, number of movement errors, number of letter errors, average hand speed, and average figure-8 size) in *experiment 2* were not different from control values in *experiment 1* (all P values >0.05). These results show that distraction interfered during practice of the dual task trials but did not alter the final performance level.

TABLE 3. Average hand speed and average figure-8 size after practice and during dual task performance

Subject	Average Hand Speed			Average Figure-8 Size			Subject	Average Hand Speed			Average Figure-8 Size		
	Late	Dual task	Change (%)	Late	Dual task	Change (%)		Late	Dual task	Change (%)	Late	Dual task	Change (%)
CBL-01	977	892	-8.7	1778	1618	-9.0	CNT-01	1669	1826	9.4	1367	1471	7.6
CBL-02	828	668	-19.3	1746	1643	-5.9	CNT-02	1430	1444	1.0	1231	1313	6.7
CBL-03	819	645	-21.2	1690	1483	-12.2	CNT-03	1441	1461	1.4	1933	1783	-7.8
CBL-04	969	805	-16.9	1714	1649	-3.8	CNT-04	2044	1869	-8.6	1892	1818	-3.9
CBL-05	722	596	-17.5	1369	1333	-2.6	CNT-05	708	865	22.2	1017	1106	8.8
CBL-06	533	550	3.2	1217	1326	9.0	CNT-06	812	1065	31.2	992	1117	12.6
CBL-07	1068	1150	7.7	1837	2169	18.1	CNT-07	1972	2014	2.1	1461	1464	0.2
CBL-08	310	342	10.3	1060	1265	19.3	CNT-08	1607	1825	13.6	1795	1844	2.7
CBL-09	685	607	-11.4	1660	1824	9.9	CNT-09	1030	1061	3	1201	1221	1.7
CBL-10	1083	1165	7.6	1387	1297	-6.5	CNT-10	1566	1199	-23.4	1225	1138	-7.1
Mean ± SE	799 ± 78	742 ± 83	-6.6 ± 4.0	1546 ± 84	1560 ± 90	1.6 ± 3.6	Mean ± SE	1428 ± 143	1463 ± 128	5.2 ± 4.8	1411 ± 110	1427 ± 94	2.1 ± 2.2

Average hand speed is in mm/s. Average figure-8 size in mm/figure-8. Late, mean last five figure-8 task trials; dual task, mean of five dual task trials; change, percentage change from late to dual task.

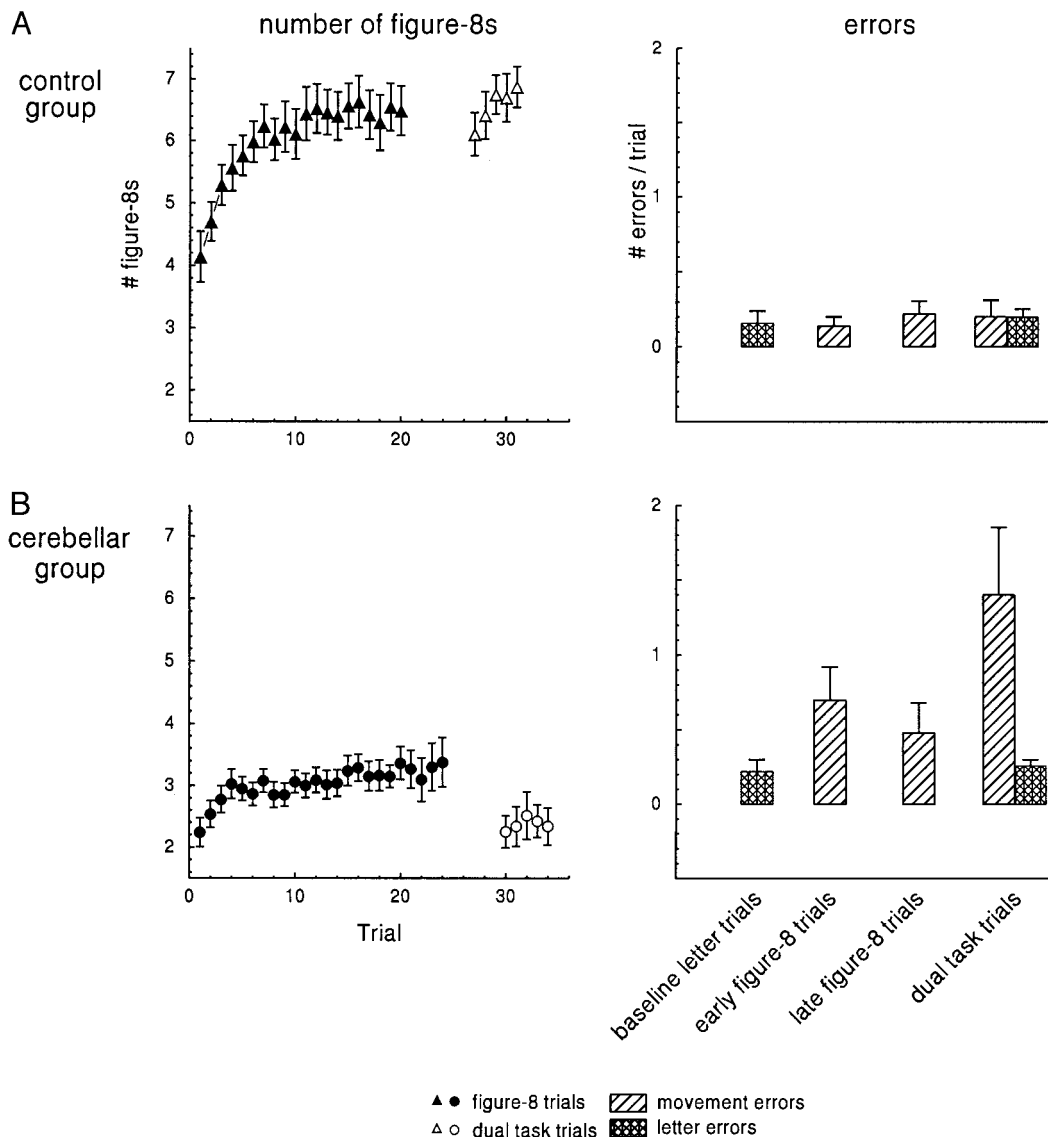


FIG. 4. Plots of group data (mean \pm SE) for the number of figure-8s and the movement and letter errors from *experiment 1*. Control group data (triangles) are shown in *A*. Cerebellar group data (circles) are shown in *B*. Closed symbols indicate figure-8 trials alone. Open symbols indicate dual task trials. Movement (striped bars) and letter errors (hatched bars) are averaged (\pm SE) in 5 trial blocks, where early is the average of the first 5 trials and late is the average of the last 5 trials.

DISCUSSION

The cerebellar group that we studied showed a small amount of improvement in motor performance after practicing the figure-8 task. Motor performance was degraded to prepractice levels when cerebellar subjects focused their attention away from the movement during dual task trials. This was true even when cerebellar subjects performed an easier version of the movement task (i.e., circles instead of figure-8s). In contrast, control subjects greatly improved the movement when they practiced the figure-8 task alone. Controls did not show degradation of motor performance when distracted after movement practice. They were slower to learn the movement when they were distracted during practice, indicating that interference occurred only in the unpracticed state. These findings indicate that controls could learn movement automaticity with practice. Cerebellar subjects were unable to learn to perform a novel movement in a more automatic fashion.

Mechanism of dual task interference

The degradation in cerebellar subjects' performance on dual task trials (*experiment 1*) and the slow rate of learning during control subjects' dual task practice (*experiment 2*) indicate that interference occurred between the two tasks. Why did an auditory vigilance task interfere with performance of a motor task? Dual task interference could theoretically occur at one or more of the three stages in task performance: stimulus perception, response selection, and response production (Pashler 1994). In our study, we think that interference is less likely to occur at the stimulus perception stage because the figure-8 task required visual, vestibular, and kinesthetic perception, while the letter task required auditory perception. However, some human imaging studies show that sensory input in one modality frequently decreases activation levels in areas corresponding to other modalities (Grafton et al. 1995; Jenkins et al. 1994). We also think that interference would probably not

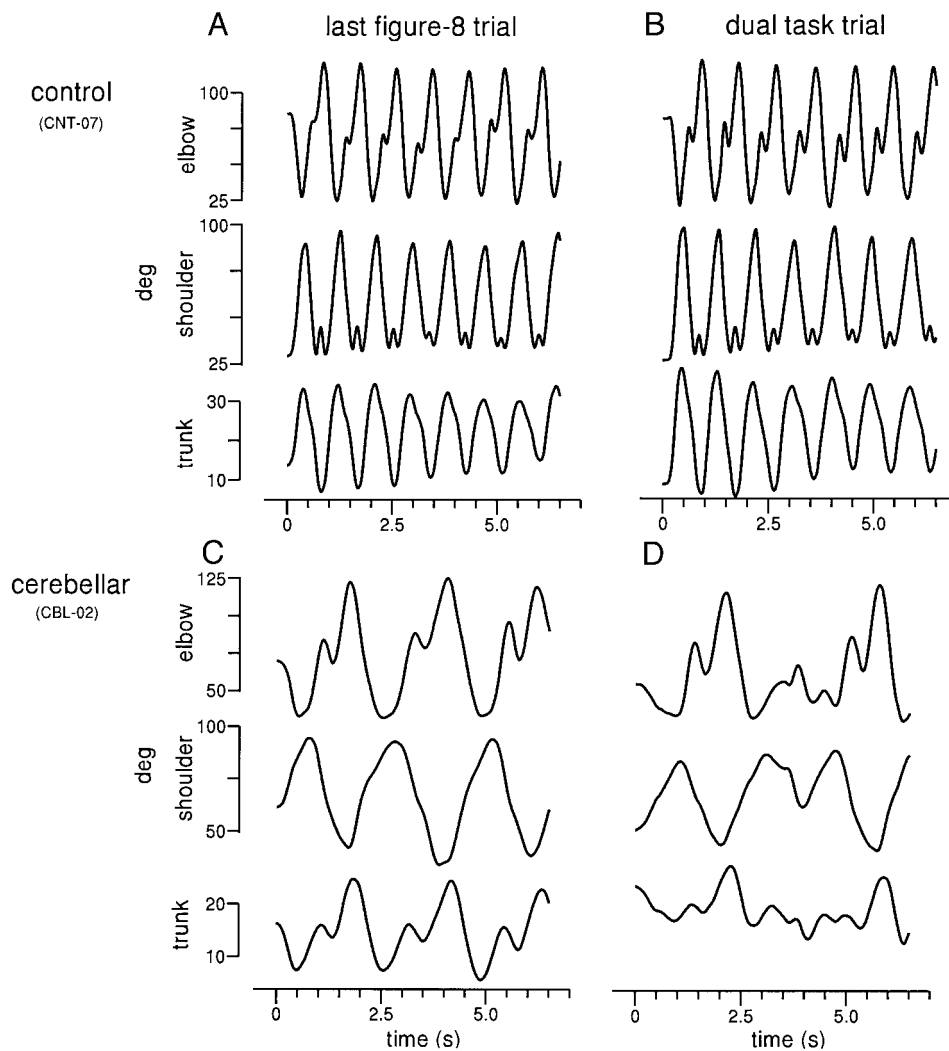


FIG. 5. Plots of joint angle versus time for a control subject and a cerebellar subject in *experiment 1*. Plots show shoulder, elbow, and trunk angle for the last figure-8 trial (A and C) and for a dual task trial (B and D). Increasing values signify flexion. Trunk angle is a measure of trunk inclination with respect to a vertical reference.

occur in the response production stage because the two tasks used different motor effectors and because the letter task response was given after the figure-8 task was completed. We speculate that interference occurred in the response selection stage. Pashler (1994) suggests that a “central bottleneck” in processing can occur during response selection. If two tasks require the same central executive resources to select the appropriate response, one task would be delayed or impaired while the other task used this resource. Interpreted in this way, our results suggest the same central executive resources are required for the cerebellar group to perform both tasks, regardless of practice. In contrast, practiced control subjects did not suffer interference between the tasks, suggesting that they have

learned to perform the motor task with no demands on central executive resources. In other words, controls could learn the motor task to the point of automaticity, but cerebellar subjects could not.

The brain regions (central executive resources) involved in response selection for these two tasks are probably not in a single, unique anatomic location (Pashler 1994). However, the primary portions of this network may be located in the prefrontal regions (Fuster 1997; Goldman-Rakic 1996). It has been proposed that the dual task interference that occurs when learning a motor task and a verb-generate task occurs in prefrontal and anterior cingulate cortex (Passingham 1996). Human imaging studies show that similar frontal areas (e.g.,

TABLE 4. Number of circles and movement errors during early, late, and dual task performance

Subject	Number of Circles				Movement Errors		
	Early	Late	Dual task	Change (%)	Early	Late	Dual task
CBL-01	4.88	5.75	4.75	-17.4	0.2	0.8	2.8
CBL-07	2.58	4.03	3.2	-20.5	1.0	1.6	2.6
CBL-08	2.92	3.63	2.95	-18.7	2.6	2.0	2.8
Mean \pm SE	3.46 \pm 0.72	4.47 \pm 0.65	3.63 \pm 0.56	-18.9 \pm 0.9	1.3 \pm 0.7	1.5 \pm 0.7	2.7 \pm 0.1

For number of circles: early, mean of first 3 circle task trials; for number of movement errors: early, mean of first 5 circle task trials; late, mean of last 5 circle task trials; dual task, mean of 5 dual task trials.

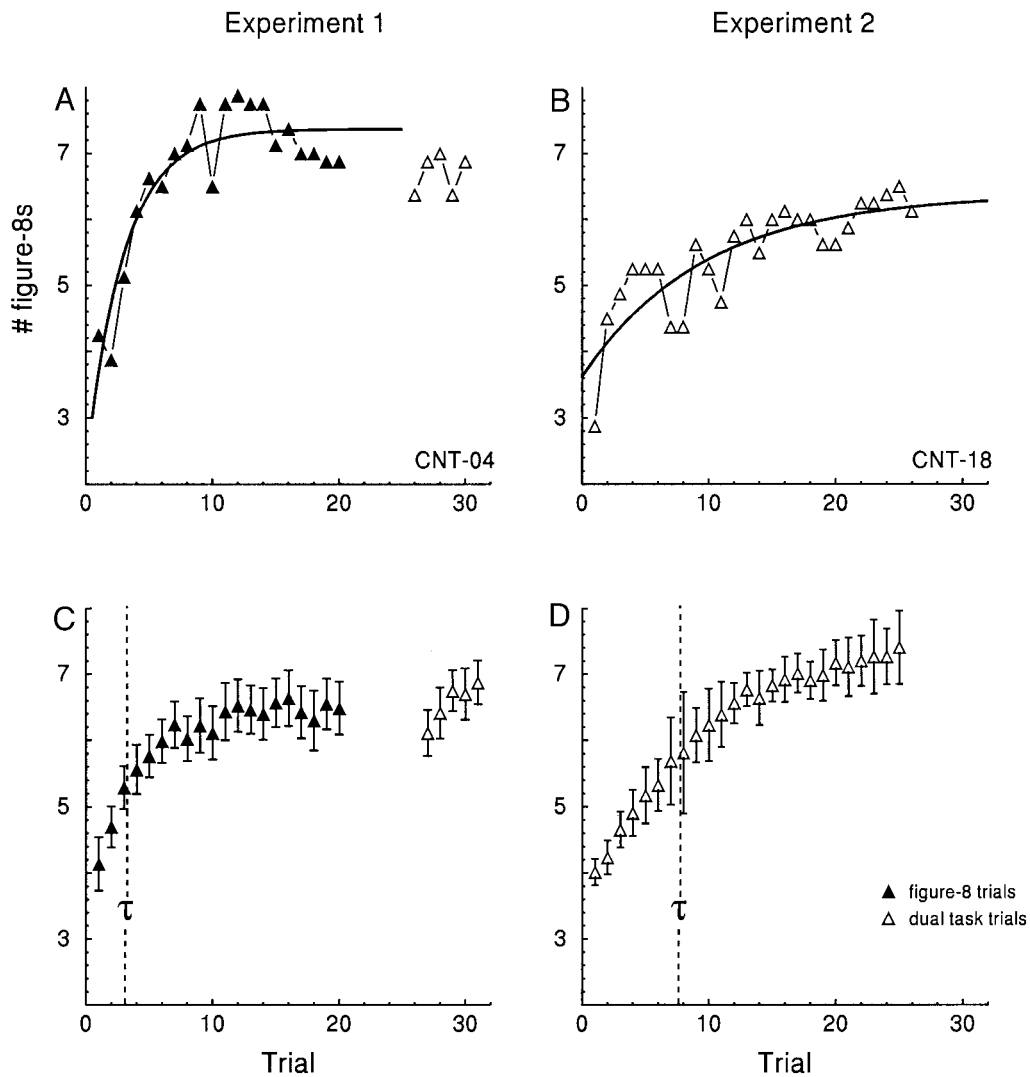


FIG. 6. Plots of the number of figure-8s for a control subject from *experiment 1* (A) versus *experiment 2* (B). Plots of group data (mean \pm SE) for the number of figure-8s from *experiment 1* (C) versus *experiment 2* (D). The large curvilinear line through the data points in A and B represent the exponential curve fits from which the rate of learning was calculated. The vertical dashed lines in C and D represent the group averages for the rate of learning (i.e., the number of trials to progress approximately two-thirds of the way through the adaptation process). Other conventions as in Fig. 3.

Brodmann's areas 32 and 46) increase activity during auditory vigilance tasks (Kawashima et al. 1999; Zatorre et al. 1999) and during early motor skill acquisition (Ghilardi et al. 2000; Honda et al. 1998; Jenkins et al. 1994; Jueptner et al. 1997a; Shadmehr and Holcomb 1997; Toni et al. 1998). Several studies have shown that prefrontal activity decreases when the

motor skill becomes over-learned (Jenkins et al. 1994; Jueptner et al. 1997a; Shadmehr and Holcomb 1997; Toni et al. 1998). We speculate that dual task interference may have occurred in our cerebellar subjects because of overlapping demands on prefrontal circuitry.

Another possibility is that dual task interference occurred in

TABLE 5. Rate of learning and asymptote for Experiment 1 versus Experiment 2

Experiment 1 (Figure-8 Task Practice)			Experiment 2 (Dual Task Practice)		
Subject	Rate of learning	Asymptote	Subject	Rate of learning	Asymptote
CNT-01	3.3	8.0	CNT-11	6.1	8.0
CNT-02	4.9	7.4	CNT-12	3.9	7.2
CNT-03	4.1	8.0	CNT-13	9.6	10.3
CNT-04	3.0	7.1	CNT-14	12.0	6.5
CNT-05	1.3	4.9	CNT-15	7.7	7.2
CNT-07	3.4	4.6	CNT-16	11.4	7.5
CNT-08	1.6	7.1	CNT-17	2.5	6.9
CNT-10	4.8	7.4	CNT-18	9.7	6.4
Mean \pm SE	3.3 \pm 0.5	6.8 \pm 0.5	Mean \pm SE	7.9 \pm 1.2	7.5 \pm 0.4

the cerebellum itself. Although the cerebellum was damaged in all subjects, the lesions were incomplete, making cerebellar function abnormal but probably not absent. Our cerebellar subjects had worse overall motor performance than control subjects in addition to the dual task interference after practice. Perhaps our results reflect an overall increase in attentional processing demands that become more apparent during dual task performance. Although the cerebellum is largely considered a motor structure, recent research suggests that part of it may play a role in cognitive processing (Allen et al. 1997; Fiez et al. 1992; Levisohn et al. 2000; Riva and Giorgi 2000; Schmahmann and Sherman 1998; Townsend et al. 1999). Ivry and colleagues have suggested that the neocerebellum may function as a timing mechanism for the CNS (Ivry and Diener 1991; Ivry and Keele 1989; Mangels et al. 1998). The cerebellum has also been implicated in the orientation of attention (Allen et al. 1997; Courchesne et al. 1994; Le et al. 1998; Townsend et al. 1999; but see Casini and Ivry 1999). Central timing control and/or attention orientation could be important in executing both the figure-8 task and the letter task.

The cerebellum and movement automaticity

Given our results, we propose two possible roles for the cerebellum in this task. One possibility is that the cerebellum is involved in shifting movement performance to a more skilled and automatic state (Doyon et al. 1998; Jenkins 1994; Thach 1998). Cerebellar damage may prevent the transformation from early to late motor skill acquisition. There is a growing body of evidence suggesting that skilled movements rely on one or more internal representation of the body and/or task and that the cerebellum may be required to change and/or store these representations (Hore et al. 1999; Kawato and Gomi 1992; Shimansky et al. 1997; Wolpert and Kawato 1998). Cerebellar damage could result in an inability to form an adequate internal representation of a motor pattern, despite practice. The idea that cerebellar damage may impair the transformation to a more automatic movement is consistent with several neuroimaging studies showing that some cerebellar activity is greatest early in motor learning tasks (Doyon et al. 1996; Jenkins et al. 1994; Jueptner et al. 1997b; Toni et al. 1998). It is also consistent with our cerebellar group's limited improvement in the movement task after practice and their degradation of movement performance to prepractice levels during dual task trials.

A second possibility is that the cerebellum is important in the execution of a more automatic movement once it has been learned. This idea is more consistent with a neuroimaging study showing that cerebellar activity is greatest when a practiced movement is performed at a later time (Shadmehr and Holcomb 1997). It may be that early performance of a novel motor task relies more on frontal cortex and practiced movement relies more on cortical and subcortical motor areas (e.g., cerebellum). If more attention-demanding movements are controlled by higher order structures (i.e., more prefrontal lobe involvement) as suggested by human imaging studies (Grafton et al. 1995; Hazeltine et al. 1997; Honda et al. 1998; Jueptner et al. 1997a), then less attention-demanding movements may rely more on adequate internal representations of the motor pattern. After cerebellar damage, frontal circuitry may not (or cannot) give up monitoring and controlling the movement. Our

data do not allow us to adequately distinguish between these two possibilities. However, we speculate that the cerebellum may be involved both in shifting movement performance to a more automatic state and in executing the movement once it has been learned. These two functions may be parts of the same continuum of cerebellar control and are not mutually exclusive.

If the cerebellum is necessary for motor skill acquisition, then why did our cerebellar subjects show some improvement in movement performance after practice? With practice, the cerebellar group increased the number of figure-8s they could perform, from 2.5 ± 0.2 to 3.3 ± 0.3 . This improvement is consistent with other studies showing impaired but not absent motor learning in some cerebellar patients (Deuschl et al. 1996; Lang and Bastian 1999; Weiner et al. 1983). A few human cerebellar studies have shown no motor learning deficits associated with certain tasks, such as drawing complex figures (Timmann et al. 1996; Topka et al. 1998) and adjusting for predictable gait perturbations (Rand et al. 1998). We speculate that the practice dependent learning observed in our cerebellar subjects may be fundamentally different from that of control subjects. This is because the cerebellar subjects improved movement performance but the movement did not become more automatic, as evidenced by dual task interference. It is possible that the motor improvement observed in the cerebellar group could be due to another mechanism, such as "priming" in other intact brain structures. However, it should be noted that this improvement in motor performance was inadequate to make the movement automatic.

We cannot draw any conclusions regarding which specific cerebellar regions are important for performance of more automatic movements. There are two reasons for this. First, both medial and lateral cerebellar regions are likely to play a role in controlling the movement during the figure-8 task. This is because subjects have to control posture and coordinate arm and trunk movement. Second, our subjects did not have lesions that were isolated to discrete parts of the cerebellum. Future studies of subjects with more discrete lesions may provide additional information about how functional divisions within the cerebellum contribute to the control of automatic movements.

In summary, we found that cerebellar subjects show marked degradation of a practiced movement when they are required to focus their attention away from the movement. Control subjects did not show movement degradation after practice. Given these results, we conclude that the cerebellum likely has an important role in shifting movement performance to a more automatic state.

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