Examining Prepotent Response Suppression in Aging: A Kinematic Analysis

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Two experiments were designed to explore how age differences in conflict detection may contribute to poorer motor performance. In each experiment, 12 young adults (YAs) and 12 older adults (OAs) performed a finger sequencing task in which the frequency of specific critical transitions was varied. These critical transitions were contrasted with violation transitions to assess the ability to detect a conflict in response requirements. In addition to accuracy and reaction time, the authors used kinematic data to parse movements into planning and motor execution phases. OAs were differentially slower to respond to violations than YAs, in line with other research on executive control, prepotent response suppression, and aging. Kinematic analyses revealed that YAs executed movements more rapidly on violation than critical transitions, whereas OAs executed movements at the same speed regardless of response predictability and increased planning time. The authors argue that OAs are unable to reprogram prepotent movement plans to overcome slowed movement planning in cognitively challenging situations. The results are discussed in terms of the influence of age-related cognitive inefficiency on motor control.

Keywords: executive control, motor control, movement kinematics, conflict monitoring, response suppression

Highly complex tasks, such as driving a car, become almost automatic or habitual because of the high frequency with which they are performed, despite the fact that they require an efficient coordination of a variety of motor and cognitive processes, including executive control. Both executive control mechanisms and motor control processes have been shown to change in later adulthood. However, little research has directly assessed how age-related decreases in executive control affect motor control. The goal of the current study was to examine this relationship by invoking *prepotent* (i.e., well-learned) motor responses. Many of the prepotent actions that compose a complex task, such as driving, may need to be modified when one is put into a novel situation. For example, individuals who are more familiar with an automatic transmission must overcome a prepotent series of actions to drive a car with a manual transmission. This ability may rest on a

number of executive control mechanisms, such as error detection or conflict monitoring, as well as motor control processes responsible for planning, executing, or terminating the appropriate series of movements. In the current study, we used kinematic measures of motor performance on a finger sequencing task to determine how age-related cognitive inefficiency might affect motor control.

Executive Control, Response Suppression, and Aging

Various definitions of executive control have been discussed in the literature (e.g., Logan, 2004; Miyake et al., 2000; Salthouse, Atkinson, & Berish, 2003; Verhaeghen & Cerella, 2002; Verhaeghen, Cerella, Bopp, & Basak, 2005). Most revolve around the concepts of coordinating, planning, monitoring, and sequencing of cognitive processes. Researchers have also shown that healthy aging is associated with deficits in executive control processes supported by the frontal lobes (West, 1996). Many tasks that have been used to show executive control deficits in aging induce and require later suppression of prepotent responses. For example, older adults (OAs) have shown more difficulty overcoming a prepotent response than young adults (YAs) on tasks, such as go/no-go (Nielson, Garavan, Langenecker, Stein, & Rao, 2001), stop-signal (Kramer, Humphrey, Larish, & Logan, 1994), and Stroop paradigms (e.g., Pilar, Guerrini, Phillips, & Perfect, 2008). The executive control demands in these tasks, as well as others (such as the Eriksen flanker [e.g., Gehring, Goss, Coles, Meyer, & Donchin, 1993] and Simon tasks [e.g., Kerns, 2006]), arise because of the need to coordinate a number of cognitive and motor processes for successful performance in the face of prepotent response preparation. We propose that a number of dissociable cognitive and motor processes contribute to accurate performance when prepotent response expectancies are violated. For example, performance on the incongruent version of the Stroop test (e.g.,

Spreen & Strauss, 2001) first involves detection of the conflict between the prepotent tendency to read the word (e.g., "blue") and the response requirement to indicate the color of ink in which it is printed (e.g., "red"). Once the conflict is detected, one must overcome the prepotent response preparation (i.e., articulating the word "blue") to prepare the appropriate response (i.e., "red"). That is, the preprogrammed response of saying the word "blue" must be reprogrammed such that "red" can be articulated properly.

In the past decade, there has been a great deal of interest in conflict monitoring (Botvinick et al., 2004) and error detection (Holroyd & Coles, 2002) processes as attentional control mechanisms that are recruited during prepotent response tasks. Recent findings have shown that such attentional control mechanisms may decline in later adulthood (e.g., Mathalon et al., 2003; Nieuwenhuis et al., 2002; Pietschmann, Simon, Endrass, & Kathmann, 2008; West, 2004). Those declines are evidenced by decreased amplitude of two event-related potential components: (a) the N450 and (b) the error-related negativity, which have been linked to the anterior cingulate cortex (ACC). In general, research suggests that age differences in the ability to detect conflicts might help explain age-related declines in the ability to overcome a prepotent response.

However, research on the processes involved in reprogramming a response during an ongoing motor plan is far less common. One example comes from Mars, Piekema, Coles, Hulstijn, and Toni (2007), who examined the brain areas involved in action reprogramming. It was shown that reprogramming a response was associated with a specific network of frontal and parietal regions. The ACC might also play a role in situations of movement reprogramming, as this structure has been implicated in the selection of actions and initiation of motor plans (for a review, see Picard & Strick, 1996). The efficiency of motor reprogramming processes with advancing age has not been thoroughly studied, nor has the involvement of such reprogramming processes in situations of prepotent response violation.

The foregoing review suggests that mechanisms that underlie prepotent response suppression include both cognitive and motor control processes. For some time it has been argued that sensory and cognitive integration is increasingly important in later adulthood (e.g., Baltes & Lindenberger, 1997; Schneider & Pichora-Fuller, 2000). More recently, researchers have focused also on the integration between cognitive and motor processing in aging (Li & Lindenberger, 2002; Sosnoff & Newell, 2006); however, the nature of that relationship is less well understood. Most of the tasks used to show an age-related decline in executive control require a motor response of some sort; however, only a few researchers have specifically addressed the role of executive control in motor tasks. For example, Krampe, Mayr, and Kliegl (2005) reported that OAs exhibited decreased performance on a rhythmic tapping task when required to overcome a prepotent response. Consistent with this finding, Potter and Grealy (2007) showed that OAs had more difficulty than YAs inhibiting prepotent responses in an everyday, gross motor task (i.e., making wiping movements with a sponge). Their analysis included a classification of the types of motor errors made by participants, and it represents one of the first attempts to consider motoric consequences of age-related executive control inefficiency. Although these studies examined age-related changes in executive control in the context of motor tasks, no studies to date have addressed this issue by combining measurement approaches from both the cognitive and motor literatures.

Measurement Approaches

Cognitive researchers commonly define *reaction time* (RT) as the time from stimulus onset to recorded response. Measurements of RT have normally been used to demonstrate age-related decline in executive functioning. An assumption of this method is that individual differences in basic sensory and motor processes are subtracted out when comparing different conditions of a cognitive test (e.g., congruent vs. incongruent versions of the Stroop test) and that any residual differences in RT reflect differences in executive control functioning. This subtraction method presupposes that sensorimotor and cognitive components of cognitive RT are modular. Alternatively, sensorimotor and cognitive processes may interact, and perhaps more so in OAs. One potential way to examine the interaction between cognitive and motor aspects of performance is to assess different aspects of movement trajectories, or movement kinematics, along with traditional cognitive measures of accuracy and RT.

The study of movement kinematics allows one to break down individual movements into meaningful components like movement planning and movement execution. Parsing movements into kinematic components has revealed that OAs are slowed in the planning of aiming movements (Haaland, Harrington, & Grice, 1993), in the time to completion of mirror drawing (Kennedy & Raz, 2005), and in the peak velocity and time-course of movement components in point-to-point reaching tasks (Ketcham, Seidler, Van Gemmert, & Stelmach, 2002). Research employing other techniques to decompose RT has also shown age-related slowing in both movement planning and execution phases (e.g., Etnier, Sibley, Pomeroy, & Kao, 2003). It is possible that OAs not only need more time to plan their movements but that they also have difficulty programming their movements to allow faster, smoother execution. Consistent with this idea, Seidler (2006) showed that YAs are better able to modify the speed with which they execute their movements than OAs to adapt to a visuo-motor perturbation. This finding indicates that reduced flexibility to modify certain movement parameters, such as velocity, might account for some of the age-related slowing in movement planning and execution.

Taken together, this literature suggests that there may be age-related declines in more than one of the cognitive and motor processes in situations of prepotent response suppression. It is likely that age-related changes in conflict monitoring contribute to the lengthened RT of OAs on these types of tasks. However, to date it is not clear whether there are changes in the ability to reprogram a movement during prepotent response suppression with age. It has also yet to be determined whether such changes contribute to slowed response latency in OAs on those tasks. Kinematic analyses provide a potential way to measure the efficacy of motor reprogramming processes on movement execution across adult age groups.

Current Experiment

In the current research, we explored the relationship between executive and motor control processes in YAs and OAs. Specifically, we addressed the effect of age-related changes in conflict

monitoring and movement reprogramming on response execution. Participants were taught an overlearned motor response during a learning phase and had to perform a response that acted against the overlearned response during a testing phase. The task was a finger sequencing task that was performed on a midi-controlled digital keyboard (Yamaha PSR-290). Response prepotency was manipulated by varying the frequency of particular pairs of key presses during learning. We analyzed performance on this task using traditional accuracy and RT measures, and by decomposing responses into planning and execution time based on movement kinematics measured with 3-D motion capture.

For RT, it was expected that OAs would perform worse than YAs on violations of very well-learned (i.e., prepotent) responses reflecting decreased executive control efficiency with age. Moreover, we expected that OAs would require more time to plan their movements to violations of prepotent responses, reflecting the increased time needed for conflict monitoring processes and movement reprogramming with age. Finally, it was expected that decreased efficiency in movement reprogramming would lead to an inability of OAs to modify the speed with which they execute movements in response to violations.

Experiment 1

Method

Participants

We recruited 12 YAs ranging from 19 to 30 ($M = 23.83$) years of age who were university students in Montreal (Quebec, Canada), and 12 OAs ranging from 59 to 75 ($M = 66.75$) years of age from the Montreal community. Of the 24 participants, there were 8 men (4 in each age group) and 16 women (8 in the YA group, and 8 in the OA group). Participants were all right handed, had no history of neurological disorder, and had no motor dysfunction. Eligible participants had less than 3 years of musical or dance training and had not practiced for the last 10 years. All participants gave informed consent and were compensated for their time. All participants were tested on four neuropsychological tests: (a) the Wechsler Adult Intelligence Scale Digit Symbol Substitution subtest (Wechsler, 1981), (b) the Extended Range Vocabulary Test (Form V2; Educational Testing Service, 1976), (c) the Halstead–Reitan Trail Making Test, Versions A and B (Reitan, 1992), and (d) the Stroop test (adapted from Spreen & Strauss, 2001). Younger and OAs performed as would be expected on the basis of previously published work (see Table 1).

Apparatus

Participants made a series of key-press responses on a midi-keyboard (Yamaha PSR-290) using four fingers of the right hand (see Figure 1). Key presses were cued by visual stimuli presented on a computer screen (17-in. [43.18-cm] flat panel). The screen displayed four 3-in. (7.62-cm) × 3-in. (7.62-cm) dark gray boxes that mapped in a one-to-one manner from left to right onto each of four marked keys. Pieces of Velcro attached to the keys provided tactile feedback to aid participants in positioning their fingers on the corresponding keys without performing visual corrections while doing the task. Midi-data from the keyboard allowed us to measure accuracy and RT for each response. The stimulus presen-

Table 1

Means and Standard Errors of the Neuropsychological Tests and the t-test Results of the Age Group Comparisons for Each Test

Neuropsychological test	YAs	OAs
Experiment 1		
WAIS Digit Symbol***	95.08 (3.37)	70.23 (4.77)
ERVT**	10.32 (1.48)	16.74 (1.64)
Trails difference scores	29.53 (5.57)	41.57 (7.60)
Stroop interference score*	0.387 (0.04)	0.607 (0.07)
Experiment 2		
WAIS Digit Symbol***	81.15 (5.72)	53.00 (3.57)
ERVT*	8.10 (1.46)	12.85 (1.43)
Trails difference scores***	25.92 (3.48)	45.08 (4.07)
Stroop interference score*	0.497 (0.09)	0.787 (0.13)

Note. Mean scores are presented with the standard error in parentheses for the number of items completed (maximum = 133) in 2 min on the Wechsler Adult Intelligence Scale (WAIS) Digit Symbol Substitution subtest; the number of correct items, with a penalty for errors, on the Extended Range Vocabulary Test (ERVT); the difference in time (in seconds) to complete Versions B and A of the Halstead–Reitan Trail Making Test (Trails); and the difference between the seconds per item completed on the Congruent and Incongruent versions of the color Stroop test. YAs = young adults; OAs = older adults.
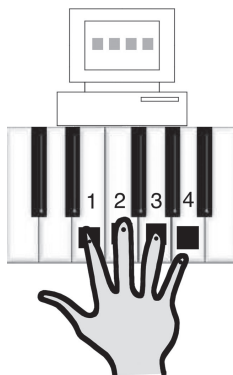* $p < .05$. ** $p < .01$. *** $p < .001$.

tation and midi-data acquisition programs were written in C# running on Version 1.1 of the Microsoft NET Framework. We recorded kinematics of the finger movements simultaneously using a 3-D motion capture system (VZ3000; Phoenix Technologies, Burnaby, British Columbia, Canada). This is an active marker system in which light-emitting diode (LED) makers are used to track the *x*, *y*, and *z* positions of each of the fingers (acquisition rate = 50 Hz).

Stimuli and Procedures

The task involved implicit learning of particular pairs of key presses (transitions between two specific fingers) embedded within 10-element sequences of quasi-randomized key presses. Key-press sequences were cued by four boxes on the computer screen that mapped onto four marked keys on the keyboard. Participants placed their four fingers on top of the four keys and were informed that each finger mapped to each of the boxes in a one-to-one manner from left to right (see Figure 1). For all sequences, the stimulus duration was 600 ms, and the interstimulus interval (ISI) was 600 ms, with a 3,000-ms pause between each sequence. The structure of the sequences differed depending on the phase of the experiment (practice, learning, or testing trials), as we describe below.

The first practice sequence was a simple, 12-element sequence (1, 2, 3, 4, . . .) that oriented participants to the box-to-key-to-finger mappings. All other practice sequences were 10 elements long, and the required key press at each serial position was randomized, except for the following criteria: the same key was not repeated in succession, and no transition (pair of key presses) was repeated in a single sequence (e.g., 2, 3, 1, 4, 3, 4, 1, 2, 4, 2).

Examples of key press sets from learning and testing blocks		
Condition	Learning Phase	Testing Phase
1-Rep	3 4 3 1 2 1 4 1 3 2	**2 4** 1 4 3 1 3 4 2 1
3-Rep	4 2 3 1 2 3 4 3 2 3	4 1 **2 1** 4 3 1 3 2 3
5-Rep	3 4 3 4 3 4 3 4 3 4	2 1 4 3 4 1 3 2 4 2

Note: Critical transitions are underlined and violation transitions are in bold.

Figure 1. Illustration of the computer/keyboard setup for the motor task (top panel). The participant placed each of the four fingers of his or her right hand on Velcro pads affixed to four consecutive keys on the keyboard. One light-emitting diode (LED) marker was placed on each fingernail of the right hand, and nine motion capture cameras were oriented in a semicircle around the computer/keyboard setup. Numbers on the keys are for illustration purposes only. The table (bottom panel) presents examples of the sequences used in each phase of the experiment. 1-Rep = one-repetition condition; 3-Rep = three-repetition condition; 5-Rep = five-repetition condition.

Sequences for the learning blocks were 10 elements long and included pairs of key presses called *critical transitions*. Across three blocks, the repetition of these critical transitions was manipulated such that they were presented either once, three times, or five times within each sequence (producing one-repetition [1-Rep], three-repetition [3-Rep], and five-repetition [5-Rep] conditions, respectively). The serial position of the critical transitions within the 10-element sequences was determined randomly. All key presses in the other serial positions were chosen randomly, except that no key press was presented in succession, and the first key press from the critical pair was not used as the first press of another pair. Each pair of key presses that was not a critical transition is referred to as a *noncritical transition*. Figure 1 presents example sequences from each of the three learning blocks. We assumed that critical transitions in the 5-Rep condition would be the most well-learned because they were more frequently repeated than in the other conditions.

For the testing blocks, each 10-element sequence included one presentation of the critical transition from the corresponding learning block and one violation of that critical transition. These violation transitions started with the same key as the critical transition but ended with a key going in the opposite direction on the hand (e.g., if a critical transition was middle finger, ring finger, then a violation would be middle finger, index finger). All other key presses were chosen randomly with the same restrictions as the learning blocks. The serial position of each critical and violation transition was selected randomly, and the critical transition could either precede or follow the violation. Examples of testing block sequences are also provided in Figure 1.

Participants were given three practice blocks to ensure that they were comfortable with the task prior to the experiment. On the last practice block, participants had to achieve a criterion of 85% correct key presses in two consecutive trials after a minimum of five trials had been completed so that all participants started the experiment with relatively equal performance on the task. There were no differences in the number of trials for YAs ($M = 7.08$) and OAs ($M = 7.08$) to reach criterion, $t(22) = -1.07$, $p = .29$. After the practice session, each participant was presented with the three learning blocks, each paired with its respective testing block as described above. The order of presentation of these pairs of blocks was counterbalanced such that an equal number of participants completed these pairs in each of the six possible orders. The experiment was a within-subjects design. The particular pairs of key presses used for critical and violation transitions in each block were the same across all participants. For all sequences, participants were instructed to respond by pressing the corresponding key as accurately and quickly as possible as each box changed color one at a time. They were not given any instructions to learn regularities within the sequences and were not given feedback about their performance.

Data Analysis

For all of the analyses, the different key-press transitions were assessed separately. We calculated the measurements for critical and violation transitions using the second key press of the pair as

it was primed by the learned, first key press. Accuracy was scored for each individual as the percentage of correct key presses out of the total key presses of each transition type per block. Responses were considered correct when a key press to the appropriate stimulus was recorded within the interstimulus interval. Only the first response within the interval was accepted, and additional attempts to respond were rejected. RT was calculated only for correct key presses and was defined as the time from stimulus presentation to recorded response. RT was also calculated individually as an average of each transition type in each block.

We analyzed the motion capture data to extract kinematic features using Mathworks Matlab 2007a. All algorithms were conducted relative to each participant's own performance. As shown in Figure 2, the kinematic features were movement *planning time* (time from the stimulus onset to the movement initiation) and *execution time* (time from movement initiation to full key depression). To pinpoint the movement initiation, we first identified the full key presses using a peak (i.e., trough) identification algorithm based on rate of change (velocity threshold) and actual displacement from the baseline in the vertical (z) dimension of the signal. The baseline was calculated by centering the data around zero by means of detrending (low frequency removal) and subtraction of a robust least squares fit of the data from the raw signal itself. The robust characteristic of the fit ignored outliers (full key presses) and modeled the resting or waiting position of the fingers. This was necessary to remove variability in the signal while at rest and, consequently, to allow for more general identification parameters in the peak finding algorithm. A *trough* was defined as a local minimum between two points in which the displacement was greater than two standard deviations from the baseline, representing the full key presses. To find the initiation of the movement, we used an algorithm that conducted a backward search from the identified trough for the first sample at which the rate of change was greater than -0.5 mm/ms. The kinematic variables of full key-press responses were averaged across participants in each age group and block.
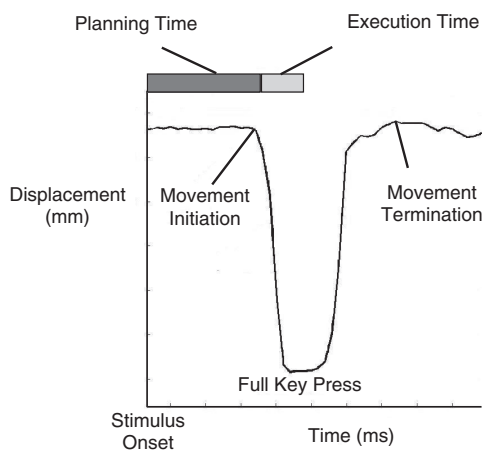

Figure 2. Illustration of the kinematic parsing of a single key-press response into its kinematic time-course components of planning time, execution time, and release time.

Results and Discussion

Keyboard Analyses

Learning blocks. Analysis of accuracy indicated that the experimental task was easy for both age groups to perform: For both YAs and OAs in all three levels of repetition (1-, 3-, and 5-Rep), accuracy was above 93.0%, with no effect of repetition or age group ($p \geq .18$).

We made planned age group comparisons on RT for each level of repetition using a Bonferroni correction to determine what frequency of repetition would be necessary to equate OAs' and YAs' latency on the critical transitions. OAs were significantly slower than YAs in the 1-Rep condition, $t(22) = -3.17, p < .01$, and the 3-Rep condition, $t(22) = -3.40, p < .01$, but there was no age difference in the 5-Rep condition, $t(22) = -1.19, p = .25$. These results suggest that OAs can perform as well as YAs if the response is highly predictable (i.e., prepotent because of repetition).

Testing blocks. To examine the effect of a need to deal with the conflict between the expected prepotent response and a violation transition, we compared critical transitions during the learning phase with violations during the testing phase. The critical transitions were taken from the learning phase because they represent optimal performance, with the greatest level of predictability. They are also free from interference from the violations, unlike critical transitions in the testing phase. YAs and OAs were highly accurate across all three conditions for violations, performing above 92%. However, given the increased cognitive demands imposed by violation transitions, participants were more accurate on critical than violation transitions, $F(2, 22) = 8.05, p < .01, \eta_p^2 = .26$ (see Figure 3).

The crucial analysis comparing RT on critical transitions to violations across repetition conditions and age groups revealed a significant three-way interaction, $F(2, 22) = 4.26, p < .05, \eta_p^2 = .28$, showing that for both YAs and OAs, responses were slower for violation than critical transitions but only in the 3-Rep and 5-Rep conditions (see Figure 3). We conducted comparisons of simple main effects to evaluate pairwise differences for each group using a Bonferroni correction. The difference between critical and violation transitions in the 5-Rep condition was larger for OAs, $M_{diff} = 241.20, F(1, 22) = 55.21, p < .001$, than for YAs, $M_{diff} = 106.64, F(1, 22) = 10.79, p < .01$. This result confirms the second hypothesis that OAs would be disproportionately slowed when encountering violations of the prepotent responses, compared with YAs.

We also sought to verify that the prepotency of the critical transitions was maintained in the testing blocks, and that the violation transitions differed from the critical transitions in the 5-Rep testing block specifically. To this end, we conducted the same analysis conducted above on RT using the critical transitions during test instead of learning. For the YAs, the average RTs for the critical transitions in the 1-Rep, 3-Rep, and 5-Rep testing blocks were $M = 498.80, SE = 11.21; M = 475.43, SE = 38.71;$ and $M = 490.77, SE = 16.69$, respectively. For the OAs, the average RTs across the same three blocks were $M = 598.74, SE = 24.71; M = 619.48, SE = 29.43;$ and $M = 569.74, SE = 27.55$, respectively. The analysis of variance (ANOVA) revealed a significant three-way interaction, $F(2, 22) = 7.09, p < .01, \eta_p^2 =$
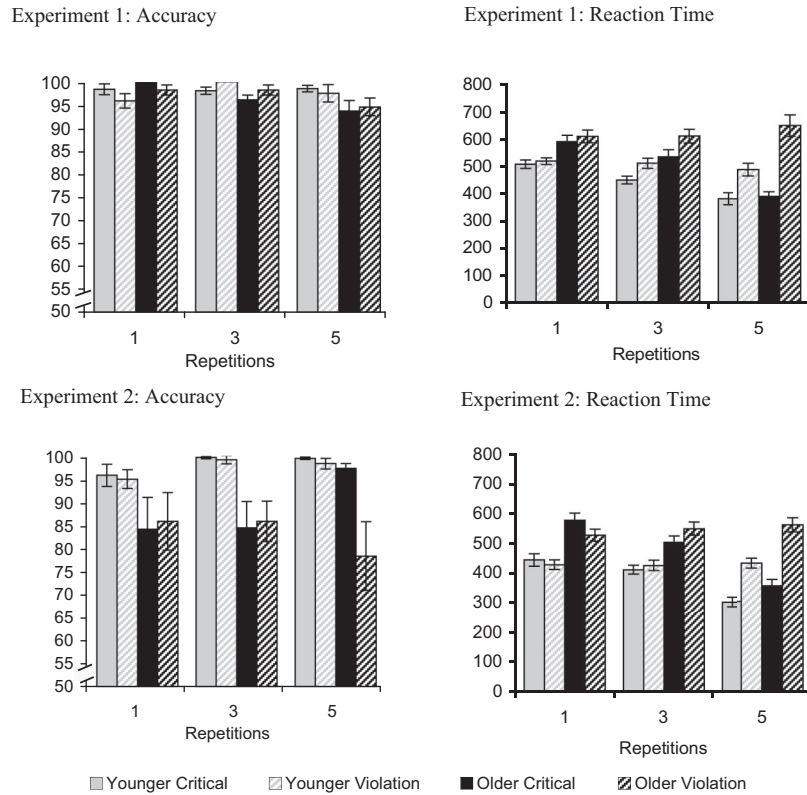
Figure 3. Younger and older adults' results from the keyboard data in Experiment 1 (top panels) and Experiment 2 (bottom panels) for critical transitions during learning blocks and violations during testing blocks for each level of repetition. Error bars represent standard error of the mean.

.40, such that OAs were significantly slower on the violations than critical transitions during the 5-Rep block, $M_{diff} = 84.48$, $F(1, 22) = 23.65$, $p < .001$, but no other comparisons were significant ($p \geq .18$). Despite the fact that all participants were slower to perform the critical transitions during the testing blocks compared with the learning blocks because of interference effects, OAs were still disproportionately slower on violation transitions. This finding corroborates the earlier interpretation that the violations were more difficult, leading to longer RTs for OAs than for YAs. Because the critical transitions during learning represent the most prepotent responses—as they are highly predictable and free from interference from the random and violation transitions—all subsequent analyses compare the critical transitions from the learning phase to the violations in the testing phase.

Noncritical transitions. To ensure that the noncritical transitions really were unpredictable random transitions, we compared the accuracy and RT for noncritical transitions between YAs and OAs across the 1-Rep and 3-Rep learning blocks. It was confirmed that there were no significant differences in accuracy or RT ($p \geq$ .23), except that OAs ($M = 604.65$, $SE = 26.05$) were slower overall than YAs ($M = 506.79$, $SE = 16.12$), $F(1, 23) = 10.74$, $p < .01$, $\eta_p^2 = .35$. Similarly, noncritical transitions during the testing blocks showed no significant effects ($p \geq .16$), except that OAs ($M = 611.93$, $SE = 27.04$) were slower overall than YAs ($M = 510.71$, $SE = 14.94$), $F(1, 23) = 11.48$, $p < .01$, $\eta_p^2 = .33$.

Kinematic Analyses

Given that OAs were slower than YAs when responding to violations of the prepotent responses in the 5-Rep condition, the kinematic data were analyzed to determine whether there were age differences in planning and execution time, respectively, that could account for the observed RT effects. We conducted these analyses using 2×2—Age Group $\times$ Transition Type (critical transitions during learning compared with violations during testing)—mixed factorial ANOVAs limited to the 5-Rep condition. Consistent with the expectation that violations would impose increased demands on cognitive control processes, movement planning time was found to be significantly longer for the violation transitions overall, $F(2, 20) = 4.75$, $p < .05$, $\eta_p^2 = .18$. In addition, there was a trend toward longer movement planning time for OAs than for YAs regardless of transition type, $F(1, 21) = 4.052$, $p = .057$, $\eta_p^2 = .16$ (see Figure 4).

Analysis of movement execution time also revealed a significant main effect of transition type, such that execution time was longer for critical than for violation transitions, $F(1, 21) = 6.05$, $p < .05$, $\eta_p^2 = .22$. Interestingly, there was also a marginally significant interaction between age group and transition type, $F(2, 20) = 3.98$, $p = .059$, $\eta_p^2 = .16$. Bonferroni corrected comparisons indicated that YAs executed violations more quickly than critical transitions, $M_{diff} = 36.26$, $F(1, 22) = 10.37$, $p < .01$, whereas OAs' responses did not differ across transition types (see Figure 4). Thus, for YAs,
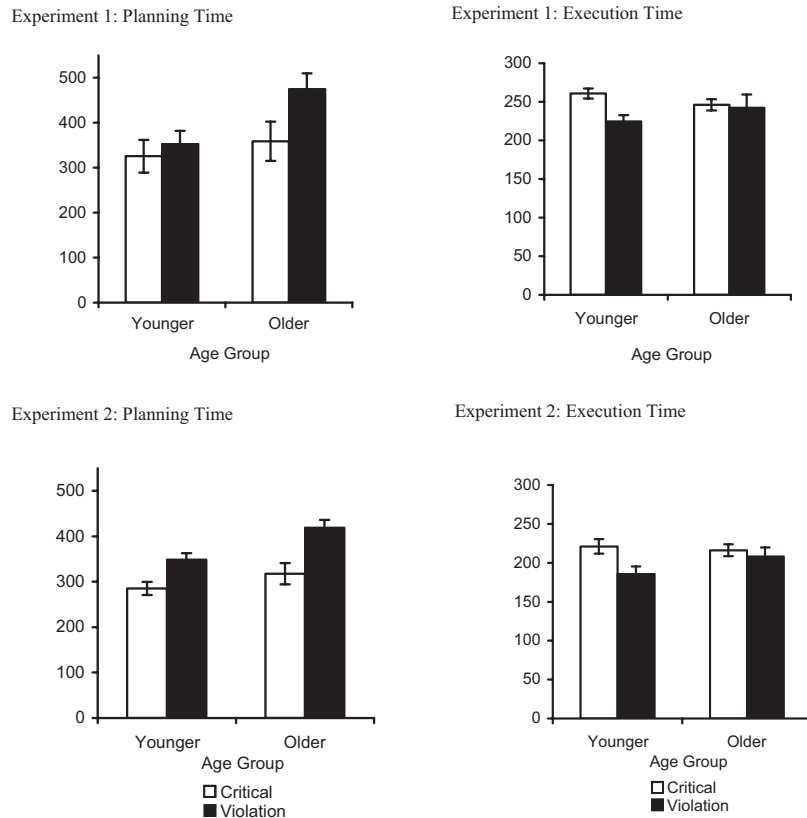
Experiment 1: Planning Time

Experiment 1: Execution Time

Experiment 2: Planning Time

Experiment 2: Execution Time

□ Critical
■ Violation

□ Critical
■ Violation

Figure 4. Results of the kinematic analysis of the five-repetition condition for younger and older adults in Experiment 1 (top panels) and Experiment 2 (bottom panels) for critical transitions during learning blocks and violations during testing blocks. Error bars represent standard error of the mean planning and execution time.

longer time spent planning the response to a violation transition was accompanied by a shorter time executing the response. This pattern of movement kinematics was not observed for the OAs.

In summary, when presented with a violation of a highly prepotent response, OAs were disproportionately slowed compared with YAs in terms of latency. This is consistent with previous studies of aging and executive control processes (e.g., Ettenhofer, Hambrick, & Abeles, 2006; MacPherson, Phillips, & Della Salla, 2002; Souchay & Isingrini, 2004; West, 1996). However, a rival explanation for the current RT data is that the increased latency to respond to a violation transition was due to the novel nature of that transition rather than the need to overcome the prepotent critical transition per se. We considered this rival hypothesis by comparing the violation transitions during the 5-Rep testing block with the completely novel and unpredictable noncritical transitions. If the violations were no different than a novel transition, then the RT for both transitions should not differ for either age group. An Age Group $\times$ Transition Type (noncritical vs. violation) ANOVA revealed a significant interaction, $F(1, 22) = 10.61$, $p < .01$, $\eta_p^2 = .33$. Post hoc comparisons revealed that YAs were marginally faster on violations than noncritical transitions ($M = 511.54$, $SE = 17.32$), $M_{diff} = -24.14$, $F(1, 22) = 4.27$, $p = .051$, whereas OAs were significantly slower on the violations compared with the noncritical transitions ($M = 624.57$, $SE = 22.99$), $M_{diff} = 29.65$, $F(1, 22) = 6.45$, $p < .05$. These findings do not support the rival

hypothesis that violations were treated simply as novel occurrences; rather, they support the above interpretation that OAs have more difficulty dealing with the violation because of the need to overcome a prepotent response tendency.

The motion capture analysis in the current experiment revealed that OAs and YAs exhibited different kinematic signatures in responses to violation transitions. Specifically, OAs spent more time planning their movements than YAs, indicating that cognitive processing was more time consuming for them. Additionally, on violation transitions, YAs shortened the execution phase of the response to optimize performance (or in other words, reduce the effect of the violation on response latency). In contrast, OAs spent the same amount of time executing movements for both critical and violation transitions, as though unable to adapt their execution time to violation responses. Thus, the inability of OAs to reprogram their movements for faster execution on prepotent response violations provides a plausible explanation for their disproportionately longer RT.

One challenge to this interpretation is that YAs exhibited longer execution time on critical transitions than OAs. This leaves open the possibility that YAs had more room to increase the speed of execution on violation compared with critical transitions. One way to evaluate this alternative explanation is to equate YAs' and OAs' execution times on critical transitions by increasing the time pres-

sure for key-press responses. We conducted a second experiment to achieve this goal.

Experiment 2

The second experiment was conducted to extend and replicate the findings of Experiment 1 by increasing the executive control demands of the task through increased speed. It was hypothesized that increasing the speed with which participants had to respond would decrease the amount of time that YAs spent executing the critical transitions, thus equating them with OAs. If our interpretation of the findings from Experiment 1 is correct and YAs are able to reprogram the speed of execution of their response in the face of a prepotent response violation, then the finding should be replicated despite shorter execution time of YAs on critical transitions in Experiment 2.

Method

Participants

We recruited 12 YA university students from Montreal (ranging from 20 to 30 years of age; $M = 23.6$ years old) and 12 OAs from the Montreal community (ranging from 62 to 75 years of age; $M = 66.5$ years old) using the same inclusion criteria as in Experiment 1. There were 9 women and 3 men in the YA group, and 11 women and 1 man in the OA group. The same battery of neuropsychological tests was used as in Experiment 1 and showed that participants were performing as would be expected for their age group (see Table 1) given previous research.

Apparatus, Task, and Procedures

The second experiment used the same apparatus as the first experiment. Test apparatus and materials were identical to those used in Experiment 1 (see Figure 1), with the only change in motion capture data collection procedures being an increase in sampling rate from 50 to 100 Hz to ensure reliability of the kinematic data. The fingers used for each transition type were counterbalanced across blocks and participants to ensure that the kinematic findings of Experiment 1 were generalizable to a variety of key-press pairs. To increase the pace of the experiment, we decreased both stimulus duration and ISI from 600 ms in Experiment 1 to 400 ms in Experiment 2. As in Experiment 1, participants continued with the experimental session after reaching a criterion of 85% correct for two consecutive trials in the last practice block. Again, there were no differences in number of trials to reach criterion between YAs ($M = 7.17$) and OAs ($M = 7.67$), $t(22) = -1.42$, $p = .17$.

Data Analysis

The keyboard data were analyzed with the same custom software as Experiment 1. Likewise, the analysis of the motion capture data followed the same technique for parsing movements into kinematic components (see Figure 2).

Results and Discussion

Keyboard Analyses

Learning blocks. As in Experiment 1, YAs were above 95% accurate on critical transitions in all conditions. However, with increased presentation rate in this experiment, OAs were less accurate overall than YAs, $F(1, 22) = 6.58$, $p < .05$, $\eta_p^2 = .23$, and there was a significant interaction between age group and repetition, $F(2, 21) = 3.66$, $p < .05$, $\eta_p^2 = .26$ (see Figure 3). Specifically, post hoc analyses that used a Bonferroni correction revealed that OAs were as accurate as YAs in the 1-Rep block ($M_{diff} = 5.8$, $p = .16$) and in the 5-Rep block ($M_{diff} = 5.8$, $p = .06$) but not in the 3-Rep block, $M_{diff} = 12.8$, $F(1, 22) = 6.35$, $p < .05$. These results suggest that the task was sufficiently more difficult for OAs in Experiment 2 to induce more errors, but performance remained well above chance.

Again, planned comparisons between the age groups on latency data at each level of repetition with a Bonferroni correction confirmed that OAs were only slower than YAs on the 1-Rep, $t(22) = -4.40$, $p < .001$, and 3-Rep, $t(22) = -3.67$, $p < .01$, conditions. That is, OAs only responded as quickly as YAs in terms of RT during the 5-Rep condition, $t(22) = -2.06$, $p = .052$. This result replicates the finding from Experiment 1 that OAs can perform a series of key presses as quickly as YAs when the responses are highly predictable.

Testing blocks. As in the first experiment, participants were more accurate when responding to critical transitions than violations, $F(2, 21) = 7.05$, $p < .05$, $\eta_p^2 = .24$. However, OAs were less accurate than YAs overall, $F(2, 21) = 9.34$, $p < .01$, $\eta_p^2 = .30$, supporting the conclusion that the increased time pressure increased task difficulty for OAs. No interactions reached significance ($p \geq .07$).

For RT, participants were also slower to respond to violations than critical transitions, $F(1, 22) = 99.27$, $p < .001$, $\eta_p^2 = .82$. OAs were slower than YAs to respond overall, $F(1, 22) = 21.68$, $p < .001$, $\eta_p^2 = .50$, and there was a significant main effect of repetition, $F(2, 21) = 60.17$, $p < .001$, $\eta_p^2 = .85$. In addition, there was a significant interaction of transition type and age group, $F(1, 22) = 5.12$, $p < .05$, $\eta_p^2 = .19$; a significant interaction of transition type and repetition, $F(2, 21) = 34.72$, $p < .001$, $\eta_p^2 = .77$; and a significant three-way interaction of transition type, repetition, and age group, $F(2, 21) = 3.84$, $p < .05$, $\eta_p^2 = .27$. Specifically, YAs were only slower to respond to violations than critical transitions during the 5-Rep block, $M_{diff} = 127.87$, $F(1, 22) = 26.35$, $p < .001$, but OAs were faster on violations in the 1-Rep block, $M_{diff} = 50.02$, $F(1, 22) = 12.83$, $p < .01$, and slower on the violations than the critical transitions in the 3-Rep block, $M_{diff} = 46.05$, $F(1, 22) = 10.69$, $p < .01$, and the 5-Rep block, $M_{diff} = 204.36$, $F(1, 22) = 67.31$, $p < .001$. As in Experiment 1, YAs and OAs exhibited the greatest slowing on violation transitions during the 5-Rep block (see Figure 3), that is, when the critical transition was the most prepotent, but the effect was more pronounced in the elderly group.

As in Experiment 1, we repeated the above analysis using critical transitions in the test phase to determine whether the prepotency of the critical transitions was maintained in the testing blocks. For the YAs, the average RTs for the critical transitions in the 1-Rep, 3-Rep, and 5-Rep testing blocks were $M = 433.30$, $SE = 15.21$; $M = 416.55$, $SE = 15.66$; and $M = 425.10$, $SE = 12.82$, respectively. For the OAs, the average RTs across the same three blocks were $M = 538.88$, $SE = 23.69$; $M = 543.00$, $SE = 18.56$; and $M = 469.47$, $SE = 12.17$, respectively. Consistent with the first experiment, the ANOVA revealed a significant three-way interaction between repetition frequency, transition type, and age,

$F(2, 21) = 4.00$, $p < .05$, $\eta_p^2 = .28$. Post hoc comparisons that used a Bonferroni correction revealed that OAs were significantly slower on the violations than the critical transitions during the 5-Rep testing block, $M_{diff} = 89.95$, $F(1, 22) = 17.78$, $p < .001$, but no other comparisons reached significance ($p \geq .39$). Again, the RTs for critical transitions during test were longer than during learning because of interference from the novel and violation transitions, and so we conducted subsequent analyses comparing critical with violation transitions using the critical transitions during the learning phase.

Noncritical transitions. As in Experiment 1, it was confirmed that the noncritical transitions were unpredictable, as there were no significant effects across conditions for either learning or testing blocks. Again, OAs ($M = 532.49$, $SE = 15.35$) were slower overall than YAs ($M = 437.20$, $SE = 15.35$) in the learning blocks, $F(1, 22) = 19.26$, $p < .001$, $\eta_p^2 = .47$, and in the testing blocks (OAs, $M = 542.75$, $SE = 14.25$; YAs, $M = 431.99$, $SE = 14.25$), $F(1, 22) = 30.19$, $p < .001$, $\eta_p^2 = .58$. Unlike Experiment 1, OAs were also less accurate on noncritical transitions in the learning blocks, $F(1, 22) = 8.66$, $p < .01$, $\eta_p^2 = .28$, and in the testing blocks, $F(1, 22) = 11.30$, $p < .01$, $\eta_p^2 = .34$, reflecting the increased time pressure and difficulty of this experiment.

Kinematic Analyses

As in Experiment 1, analysis of the kinematic variables (see Figure 4) was restricted to the 5-Rep condition to further understand the observed interaction of age group and transition type in the RT data. Again, the violations were more cognitively demanding in that it took all participants more time to plan violation transitions than critical transitions, $F(1, 22) = 23.82$, $p < .001$, $\eta_p^2 = .56$. In addition, OAs took longer to plan their movements than YAs, $F(1, 22) = 7.97$, $p < .05$, $\eta_p^2 = .30$, regardless of transition type. In execution time, there was a significant interaction between age and transition type, $F(1, 22) = 5.70$, $p < .05$, $\eta_p^2 = .21$. Importantly, the increased speed imposed in the second experiment had the desired effect of equating the age groups on execution time for critical transitions, as the post hoc comparison revealed that YAs and OAs did not differ ($M_{diff} = 6.73$, $p = .69$). In addition, those post hoc comparisons revealed that YAs spent less time executing movements for violation transitions than for critical transitions, $M_{diff} = 35.23$, $F(1, 22) = 8.76$, $p < .01$; however, OAs did not differ in execution time between transition types ($M_{diff} = 5.84$, $p = .64$). Consistent with the findings of Experiment 1, YAs' increased planning time for violation transitions was followed by decreased execution time relative to critical transitions. Also, Experiment 2 replicates the previous observation that OAs did not reduce execution time to violation transitions. There were no main effects for age or transition type for execution time ($p \geq .10$).

Together, the findings of Experiment 2 replicate those of Experiment 1 in showing that OAs are disproportionately slowed when performing an unexpected violation of a prepotent response than YAs in terms of RT. Again, we sought to rule out the possibility that the violation transitions were slower than critical transitions because they were treated as novel responses. As in Experiment 1, an ANOVA comparing violations with noncritical transitions during the 5-Rep test block revealed a significant interaction between transition type and age group, $F(1, 22) = 4.57$,

$p < .05$, $\eta_p^2 = .18$ (see Figure 3). Post hoc comparisons revealed that OAs were significantly slower on violations than noncritical transitions ($M = 541.79$, $SE = 16.67$), $M_{diff} = 34.30$, $F(1, 22) = 6.38$, $p < .05$, whereas YAs did not differ, $M_{diff} = -7.68$, $p = .59$, between violations and noncritical transitions ($M = 431.53$, $SE = 11.78$). Again these findings support the conclusion that OAs are slower to respond to violation transitions because of the need to overcome the prepotent response specifically, rather than because of the novelty of that transition.

The replication in Experiment 2 indicates that the results of Experiment 1 are not due to an age-related difference in biomechanical dependencies of the hand, and that the finding is generalizable to various pairs of fingers. Importantly, the kinematic analysis showed that the increased time pressure in Experiment 2 led to shorter execution time for YAs on critical transitions, equating them with OAs. YAs were able to use cognitive and motor processing during the longer planning time for violation responses to ensure a faster movement execution as a way of minimizing the effect of the violation on response latency. This replication also shows that the results of Experiment 1 are not due to YAs having more room than OAs to reduce the time spent executing the movements during violation transitions.

General Discussion

Our major goal was to examine the effect of age differences in executive control processes on motor control in a cognitive/motor sequencing task requiring prepotent response suppression. In terms of traditional latency measures, it was observed that OAs were slowed to a greater extent than YAs to respond to violations of highly prepotent motor responses, despite responding as quickly as YAs on the prepotent responses. Kinematic analyses indicated that both age groups required more time to plan their movements for violation than critical transitions. YAs shortened the execution time of their movements for violations of the prepotent responses, whereas OAs did not. This age difference in kinematic signatures of prepotent and violation responses may explain the disproportionately greater condition difference in RT for OAs compared with YAs. Increasing the time-pressure placed on participants in Experiment 2 equated YAs' and OAs' execution time on critical transitions; however, YAs still reduced execution time to speed up responses to violation transitions. Below, we discuss these findings in terms of their relation to the literatures on executive control, kinematic components, and the relationship between cognitive efficiency and motor control in aging.

Our cognitive RT results are consistent with previous research showing a reduced ability of OAs to perform in situations of prepotent response suppression. The go/no-go task (Nielson et al., 2001), the stop-signal paradigm (Kramer et al., 1994), and the Stroop task (Pilar et al., 2008) have all shown age-related slowing associated with the requirement to overcome a prepotent response. These findings are compatible with the hypothesis of an inhibitory deficit in later adulthood (Hasher, Zacks, & May, 1999) and with more recent theories of age-related changes in conflict monitoring/error detection (e.g., Friedman, Nessler, Johnson, Ritter, & Bersick, 2008). Moreover, a recent theory has linked cognitive aging to age-related dopamine loss (Bäckman, Nyberg, Lindenberger, Li, & Farde, 2006), and dopamine has been linked to error processing/conflict monitoring and the ACC (Holroyd & Coles, 2002).

All of the prepotent response tasks discussed above include the requirement of a motor response, and most of them require participants to withhold a motor action. However, tasks, such as the Stroop task and the current task, require participants to perform an alternative action rather than to simply withhold their response. Thus, motor processes that allow the reprogramming of prepotent response plans contribute to our ability to successfully perform these types of tasks. Yet, little research has addressed age-related differences in the ability to modify an ongoing motor program. The current study represents one of the first to address changes in the ability to modify movement parameters in response to a cognitive perturbation (i.e., a violation of a prepotent response). At present, it is not clear whether our observed results are due to age-related differences in the efficiency of processes for error/conflict monitoring, response programming/reprogramming, or both. However, in using motion capture to break down responses into planning and execution time, we can at least shed some light on the effect of cognitive inefficiency with age on motor response execution.

A central aim of the current study was to decompose RT into planning and execution time. Here, we showed that part of the age-related increase in latency to respond resulted from the fact that OAs needed longer to plan their movements than YAs in general. This finding is consistent with previous research on planning time using a variety of tasks (e.g., Amrhein, Stelmach, & Goggin, 1991; Bellgrove, Phillips, Bradshaw, & Gallucci, 1998; Era, Jokela, & Heikkinen, 1986; Haaland et al., 1993; Kennedy & Raz, 2005; Ketcham et al., 2002; Morgan, Phillips, Bradshaw, & Mittingley, 1994). It is also consistent with electromyography (EMG) literature showing that OAs exhibit longer premotor time (Etnier et al., 2003), which is quite similar to planning time as defined here. These authors also showed that motor time, from first discernable EMG activity to initiation of the movement, is not age sensitive. This is important, as it shows that movement preparation is more sensitive to the effects of aging than the transmission of the motor signal from the brain to the effector. That is, the cognitive processing involved in programming a movement likely drives much of the age difference in planning time. This suggestion is also consistent with motor control research showing that OAs are slower to discard a prepared action and to organize a new response (Amrhein et al., 1991). Increased planning time in OAs is likely attributable to changes in the efficiency of one or more executive control processes, including conflict monitoring, and motor processes involved in movement reprogramming.

In terms of the time to execute a movement, the current findings are not entirely compatible with previous research. Rather than showing overall slowing in execution time, OAs in the current experiments were only slower than YAs to execute movements when a prepotent response was violated. One interpretation of these findings is that inefficient cognitive processing during planning time prevents OAs from modifying the execution of their responses to perform optimally. In contrast, YAs were able to adjust their movement execution to VTs—a finding that is consistent with previous research showing that YAs are better able to modify movement velocity than OAs (Seidler, 2006). We interpret this finding as showing that YAs, but not OAs, use the information gained during longer planning times for violation transitions to ensure faster execution, thus minimizing the effect of prepotent response suppression on RT. Given this interpretation, one would predict that YAs should exhibit a negative correlation between

planning and execution time, whereas OAs should exhibit a positive or null correlation. In fact, these predictions were substantiated by within-age-group, one-sample t-tests comparing the average individual Fisher r to z transformed correlations between planning and execution time on violations in the 5-Rep block against zero. The average z-transformed correlation between planning and execution time for YAs was significantly less than zero in Experiment 1 ($M_{zr} = -0.46$), $t(11) = -2.51$, $p < .05$, and in Experiment 2 ($M_{zr} = -0.14$), $t(11) = -2.48$, $p < .05$, but it was not statistically different from zero for OAs in either Experiment 1 ($M_{zr} = -0.22$), $t(11) = -1.91$, $p = .085$, or Experiment 2 ($M_{zr} = 0.04$), $t(11) = 0.19$, $p = .85$. Together, these findings support the idea that YAs are more flexible in adapting movement parameters than OAs, which may explain why OAs are disproportionately slowed by cognitive manipulations compared with YAs when conventional RT measures are considered.

Current theories suggest that the conflict monitoring system, supported by the ACC, may provide the feedback necessary to allow for adjustments in cognitive control that will allow learning and avoidance of conflict in the future (Botvinick, 2007). In fact, research in support of this view has shown that ACC activation correlates with top-down cognitive control on subsequent trials in both the Stroop and Simon tasks (Kerns, 2006; Kerns et al., 2004). An extension of this theory would be that the conflict monitoring system provides feedback that can be used online for movement reprogramming in the face of a violation of a prepotent response plan. It has been shown that YAs have the ability to reprogram a response in the context of an ongoing movement plan and that this ability is supported by a dissociable network of brain areas from those involved simply in movement programming (Mars et al., 2007). Fewer studies have addressed the ability of OAs to reprogram a response. One exception is a study showing that OAs produce less efficient aiming movements when required to reprogram a response (Bellgrove et al., 1998). Specifically, when faced with the need to reprogram a response, OAs made more submovements to reach their target as a result of less precise movement trajectories than YAs. Moreover, this age difference in the ability to reprogram a response accounted for some of the age-related slowing in aiming movements.

By integrating standard cognitive measures (RT, accuracy) and kinematic analyses (planning time, execution time) in the same study, we were able to consider how age-related cognitive inefficiency affects motor control processes and how this relationship contributes to disproportionately slowed RT for OAs on violations of prepotent responses. Our results show that OAs are unable to use additional time spent planning violations of prepotent responses to ensure faster execution that would minimize the effect of the violation on RT. When confronted with the requirement to produce a motor response that acts against a prepotent response, one must process the conflict and reprogram the prepotent response plan to prepare the appropriate action. Less efficient performance in OAs may result from inefficient executive processing directly impacting the ability to reprogram a response plan. Specifically, if the conflict in response requirements is not detected as efficiently in OAs, then feedback about that conflict may not help drive the appropriate reduction in execution time.

A slightly different, but equally plausible, explanation is that the executive control processes required for planning are not yet complete prior to the execution of the movement in OAs. That is,

the computations associated with conflict monitoring and/or movement reprogramming may still be operating while OAs are executing their movements. Thus, the slower movement execution of OAs may be a carryover effect from inefficient cognitive processes or processes involved in motor preparation. The current study cannot settle the debate between these two views, but in either case, the present results are compatible with other work on aging and cognitive–sensorimotor interactions (Li & Lindenberger, 2002; Sosnoff & Newell, 2006) in showing that there is a greater interdependence of sensorimotor and cognitive processes with age.

In conclusion, the evidence provided in this study suggests that aging is associated with (a) decreased cognitive processing efficiency during response planning, and (b) a decreased ability to modify motor plans in response to increased executive control demands. These findings support the view that cognitive and motor processes interact and possibly overlap, and that this relationship changes with age.

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