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# Context-Updating Processes Facilitate Response Reprogramming in Younger but not Older Adults

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The current study used concurrent acquisition of motion capture and event-related potential (ERP) data to test the prediction that response reprogramming relies on context-updating processes, and that age differences in conflicting-response performance are related to context-updating deficits in the elderly. Participants performed a motor sequencing task that included prepotent pairs of key presses, and conflicting pairs that started with the same first key press of the prepotent pair, but ended in an unexpected alternate response. ERP analyses were used to measure the P3b component as an electrophysiological correlate of context updating. The results revealed an age-related reduction in the ability to reprogram a response as younger, but not older, adults exhibited a negative correlation between planning and execution time for conflicting responses, such that shortened execution time led to better performance by the younger group. Both age groups demonstrated a large P3b component following conflicting, but not prepotent stimuli. The peak of this P3b was delayed, and its amplitude reduced in the older, compared with younger, adults. Noteworthy was that conflicting responses with faster execution time were associated with a larger P3b component than responses with slower execution time in younger, but not older, adults, suggesting that better context updating led to more efficient response reprogramming. These findings are novel in showing that context updating is associated with adjustments in response execution, and that older adults were less able to use these context-updating processes to support successful movement reprogramming.

*Keywords:* cognitive control, response reprogramming, event-related potentials, movement kinematics, updating

The ability of older adults to manage stimulus and response conflict is thought to be a key component of age-related declines in cognitive control. Typically, older adults perform more poorly than younger adults on tasks that require conflict processing (e.g., a Stroop task). Recent findings have led to the speculation that this performance decline is related not only to less efficient conflict-monitoring processes, but also to age-related difficulties in flexibly adapting movement execution, or reprogramming a response, during tasks requiring cognitive control (e.g., Trewartha, Endo, Li, & Penhune, 2009; Trewartha, Penhune, & Li, 2011). However, recent theories have also proposed that working-memory updating plays a role in age-related cognitive control declines (e.g., Braver & West, 2008). To provide information about the cognitive mechanisms underlying response reprogramming, we used concurrent electroencephalogram (EEG) and motion-capture recordings. This allowed us to explore the potential roles of conflict monitoring as indexed by the N2 event-related potential (ERP) component, and context updating as indexed by the P3b component, in response reprogramming; see the Context Updating and the P3b Component section below for more on the P3b. We observed a P3b component following conflicting stimuli that was attenuated in the older, compared with younger, adults, and a centro-posterior N2 in the older adults only. These observations support the idea that working memory is updated with new information upon encountering conflict that ultimately facilitates response reprogramming, but that age-related differences in response reprogramming are related to declines in working-memory updating with aging.

## Cognitive Control and Aging

Cognitive control refers to the ability to plan, organize, and monitor cognitive operations through the allocation of mental resources. A variety of experimental paradigms have been used to investigate cognitive control, including the Stroop (Stroop, 1935), Eriksen flanker (Eriksen & Eriksen, 1974), Simon (Simon & Rudell, 1967), stop-signal (Logan & Cowan, 1984), and go/no-go (Donders, 1868/1969) tasks. The common element in these tasks is the need to overcome an existing prepotent response, which can be defined as any stimulus–response or response–response association that has become automatic. Cognitive control processes are thought to diminish with aging, as older adults are often slower and

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make more errors than younger adults when overcoming a prepotent response (see Braver & West, 2008 for a review). Those age differences have been attributed to an age-related decline in the ability to update working memory with task-context information (e.g., Braver & West, 2008).

We recently conducted a series of experiments to investigate age differences in the ability to overcome a prepotent response tendency through response reprogramming. Specifically, we developed a multifinger sequencing task and used motion-capture recordings to conduct kinematic analyses of prepotent response suppression. Briefly, participants were trained to associate a particular pair of key presses, generating a prepotent motor response, and were then presented with key presses that violate the prepotent pair. Movements were decomposed into response planning (latency from stimulus to movement initiation) and response-execution phases (from initiation to completion of the key press). For younger adults, conflicting stimuli led to longer planning times, but shorter execution times than the prepotent responses (Trewartha et al., 2009; Trewartha et al., 2011), and a negative correlation between planning and execution time. We interpreted this effect as a flexible adjustment in movement-execution parameters (i.e., response reprogramming) due to the detection of conflict. In comparison, older adults did not shorten execution time in response to conflict, and did not exhibit a correlation between planning and execution time. We previously speculated that this age difference was related to inefficient conflict-monitoring mechanisms in later adulthood that prevented online reprogramming of the prepotent response. However, upon deeper examination of the cognitive control and ERP literature, we opted to focus on context updating as a viable, alternative process for facilitating response reprogramming. The current study was designed to investigate the potential role of context updating in accounting for reduced reprogramming abilities in the elderly. Motion-capture recordings provided a measure of response reprogramming in the form of shortened execution time on conflicting responses, and a negative correlation between planning and execution time, whereas ERP recordings allowed us to measure P3b amplitude as an index of context updating.

## Context Updating and the P3b Component

Electrophysiological research has identified an important correlate of context updating in the form of a specific ERP component. The P300 is a positive deflection in the waveform occurring approximately 300 ms after stimulus presentation. The P300 has been widely studied in the literature, and has been associated with a variety of cognitive processes. Classification systems have been developed to describe distinct P300 subcomponents that differ in terms of their topography, and the experimental conditions that elicit them (see Polich, 2007; Verleger, 1997 for reviews). Updating of working memory with task-context information has been associated with a more posterior P300 subcomponent that is maximal over parietal sites, and has been labeled the P3b (Squires, Squires, & Hillyard, 1975). The P3b is elicited by a number of tasks, but it has been most extensively observed during oddball tasks. In such tasks, participants must respond to infrequent target stimuli that may be embedded within sequences of frequent nontargets, infrequent distractors, or both (e.g., Duncan-Johnson & Donchin, 1977; Sutton, Braren, Zubin, & John, 1965). The main findings indicate that P3b amplitude is sensitive to variations in subjective stimulus probability and task relevance of the stimulus. Further research has shown that the latency of the P3b varies with the time required for stimulus evaluation (e.g., Kutas, McCarthy, & Donchin, 1977). To integrate these and other findings, the context-updating theory proposed that the P3b is associated with processes involved in updating the mental representation of stimulus context in working memory (Donchin, 1981; Donchin & Coles, 1988).

It has been suggested that the P3b plays an important role in both stimulus processing and response selection/preparation (e.g., Gaeta, Friedman, & Hunt, 2003; Hohnsbein, Falkenstein, Hoormann, & Blanke, 1991; Verleger, Jaśkowski, & Wascher, 2005). The role of context updating in response-related processes is somewhat intuitive, given the importance of the interaction between the probability and task relevance of the stimulus in determining P3b amplitude (see Johnson, 1988). The association between the P3 and response-selection processes has been demonstrated using a variant of the go/no-go task (Randall & Smith, 2011). In this study, P3 amplitude was increased when a planned response had to be inhibited or changed for a new response. The association between the P3b and response-selection processes is further supported by research in elderly populations. It has been reported that the amplitude of the P3b component is diminished, and its peak delayed in the elderly, compared with younger adults, during conflict tasks (e.g., Kray, Eppinger, & Mecklinger, 2005; Polich, 1997; West, 2004). This P3b amplitude modulation with age has been largely interpreted as an age-related decline in the ability to update working memory with task context information, and is concomitant with age-related performance declines on conflict tasks (see Braver & West, 2008).

## Response Reprogramming and Aging

Despite the evidence that context updating plays a role in response-selection/preparation processes, the mechanism by which this occurs is poorly understood. One possibility is that context-updating processes allow for response reprogramming when stimulus evaluation dictates the need to abandon a prepotent response. Response reprogramming can be defined as the online modification of an already prepared motor program (e.g., Bellgrove, Phillips, Bradshaw, & Galluci, 1998; Mars, Piekema, Coles, Hulstijn, & Toni, 2007; Neubert, Mars, Olivier, & Rushworth, 2011). In response-reprogramming tasks, participants are typically cued to make one response, but before the response is executed, the response contingency is unexpectedly changed. Participants must reprogram the already prepared response with new movement parameters, such as changing the effector, the trajectory, and the velocity of the movement, in order to respond correctly. Planning the new movement requires additional processing time that delays the response, relative to conditions in which no response change is required. Successful reprogramming allows for the efficient execution of the correct alternative response. Aging has been associated with diminished response reprogramming as older adults have been observed to require more time to discard an already prepared response, and exhibit less efficient reprogrammed movements (e.g., Amrhein, Stelmach, & Goggin, 1991; Bellgrove et al., 1998). In our previous work, successful abandonment of an already programmed prepotent response similarly led to efficient execution of the conflicting response in younger adults (Trewartha et al., 2009; Trewartha et al., 2011). This reprogramming interpretation is supported by the observation of a negative correlation between the time spent planning (reprogramming) the response and the time spent executing the movement. Thus, in the current study, we operationalized response reprogramming as longer planning time, associated with shorter execution time for conflicting than for prepotent responses.

In prepotent response tasks, a conflicting stimulus will trigger the abandonment of the prepotent action plan, such that an appropriate motor plan can be prepared and executed. For example, in the classic color–word Stroop task, the prepotent tendency to read the word (e.g., RED) must be suppressed in order to respond correctly to the color in which it is printed (e.g., blue). The prepotent tendency to respond by reading the word is likely active in working memory initially, and when a conflicting stimulus is encountered, working memory must be updated with the alternative stimulus dimension before the correct response can be initiated. Thus, the occurrence of a conflicting stimulus might trigger the updating of working memory with a new stimulus–response mapping that can be used for the generation of the appropriate new motor program.

Recent approaches to studying response reprogramming in conflict tasks have been to use either electrophysiological measures of motor performance or kinematic analyses to explore motor output in response to conflict. For example, Szücs, Soltész, and White (2009) used concurrent electromyographic (EMG) and EEG recordings to explore whether conflict resolution occurs at the level of stimulus or response processing in a manual version of the Stroop task. Participants responded with either their right or left hand to competing stimulus dimensions. For incongruent trials in which stimuli cuing both left- and right-hand responses were present, muscle activity was observed in both hands, indicating that both responses were prepared. In addition they observed ERP components signaling stimulus conflict. On correct trials with slower reaction time (RT), the muscle activity in the incorrect hand diminished after the conflict was detected. This suggests that the conflicting stimulus dimensions were both processed up to response preparation at which time conflict resolution took place. Thus, it is likely that conflict processing influenced motor performance by triggering the abandonment of the incorrect, prepotent response in favor of the correct response.

## Current Study

In the current study, we investigated context updating and response reprogramming by acquiring concurrent EEG and motion-capture data. Synchronization of these recordings allowed us to explore the time course of ERPs associated with conflicting stimuli in relation to the kinematic measures of planning and execution time, providing a way to measure response reprogramming. Younger and older adults performed a modified version of the task used in our previous work, in which conflicting responses were embedded in repeated, prepotent pairs of key presses (Trewartha et al., 2011). If response reprogramming, and hence conflict resolution, requires the updating of working memory with task-context information, then conflicting stimuli should elicit a larger P3b component than prepotent responses. Given that aging has been associated with declines in context updating, we also tested the prediction that the P3b elicited by conflicting stimuli would be attenuated in the older adults. If successful context updating contributes to efficient response reprogramming, younger adults should exhibit a P3b component that is larger on trials with faster execution speed. However, if response reprogramming is diminished in the elderly due to age-related declines in context updating, this same modulation of P3b amplitude should be diminished in the older adult group.

## Method

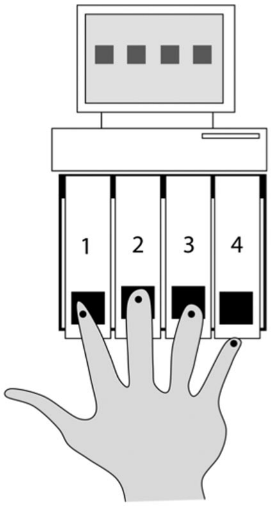
### Participants

Participants in this study were 17 younger adults (18–32 years old, $M = 22.4$, $SD = 2.8$; 11 women), and 15 older adults (66–81 years old, $M = 72.3$, $SD = 5.0$; 12 women). Participants were right-handed and free from physical and neurological conditions affecting finger or hand movements. To control for the effects of previous experience with finger-sequencing tasks, all participants were selected to have less than 3 years of musical training, and had not practiced a musical instrument in the past 10 years. Participants gave informed consent to participate in this study, which was approved by Concordia University's Human Research Ethics Committee.

### Apparatus, Stimuli, and Procedure

Participants performed a multifinger-sequencing task in which well-learned pairs of prepotent key presses were compared with conflicting key presses to investigate age-related differences in cognitive control and response reprogramming. The experimental session consisted of four different conditions: (a) random baseline, (b) prepotent baseline, (c) prepotent only, and (d) mixed. The specific stimulus sequences that comprised each condition are described below. In this task, participants produced a series of key presses in response to visual cues. No performance feedback was provided, and participants were asked to make each response as quickly and accurately as possible. Visual cues were four dark gray, 3 × 3-in. boxes presented horizontally in the center of a 17-in. flat-screen monitor, which remained on the screen throughout the entire experiment. Each box represented one of the four fingers of the right hand and mapped onto four consecutive keys on a custom response box that was built to mimic the physical properties of the keys on a standard piano-type keyboard used in our previous experiments. Pieces of Velcro affixed to each key served as a tactile cue (see Figure 1). Each stimulus involved one of the boxes changing color to indicate the key to be pressed. Each trial was defined as a 10-stimulus sequence, with each stimulus displayed for 400 ms, with a 400 ms interstimulus interval (ISI). There was also a 3,000 ms pause between each trial.

Each participant first completed a block of 15 random-baseline trials as a measure of the ability to respond to unpredictable sequences of key presses. The stimuli for these trials were pseudorandomly ordered with the constraint that no stimulus was ever repeated in succession. The second block was the prepotent baseline block, during which participants performed 15 trials that each consisted of five repetitions of a single pair of stimuli (e.g., cuing the index finger followed by the middle finger). The prepotent response itself was defined as the second response in the pair (e.g.,



*Examples of stimulus pairs in each condition*

| Condition | Example Sequence | Stimulus Type Breakdown |
|---|---|---|
| Random Baseline (15 trials) | 4 2 1 3 2 1 4 1 2 3 | 150 random stimuli |
| Pre-potent Baseline (15 trials) | 1 2 1 2 1 2 1 2 1 2 | 75 pre-potent stimuli |
| Pre-potent Only (5 blocks of 5 trials) | 1 2 1 2 1 2 1 2 1 2 | 125 pre-potent stimuli |
| Mixed (3 blocks of 20 trials) | 1 2 1 2 **1 4** 1 2 1 2 | 240 pre-potent stimuli<br>60 conflicting stimuli |

*Note: Pre-potent pairs are underlined and conflicts are in bold. Each trial is 10 key presses long.*

*Figure 1.* Illustration of the response box and task. Participants placed four fingers of their right hand on four consecutive keys on a response box. Pieces of Velcro affixed to each key served as a tactile cue to ensure that participants' fingers remained on the correct keys. One LED marker was placed on each fingernail of the right hand, and six motion-capture cameras recorded their position during the task. Numbers on the keys are for illustration purposes only. The table (bottom panel) presents examples of the sequences used in each condition, along with the numbers of each stimulus type presented.

middle finger), as this response was primed by the first response in the pair through repetition. This prepotent baseline block induced a stimulus−stimulus (or response–response) contingency that defines the prepotent response for the rest of the experiment.

The remaining blocks alternated between mixed and prepotent-only blocks. We considered the mixed blocks to be the most important condition, in that it allowed us to compare behavioral and ERP responses to conflicting and prepotent stimuli. In these blocks, a single conflicting pair was embedded within repeated prepotent pairs in each trial (similar to Trewartha et al., 2011). Each conflict block consisted of 20 trials that contained four prepotent pairs and one conflicting pair. The conflicting-stimulus pairs started with the same first stimulus as the prepotent pair, but ended unexpectedly with an alternate stimulus (see examples in Figure 1). As with the prepotent response, the conflicting response was defined as the second key press in the pair. The serial position of the conflicting pair within each trial was determined randomly, and an equal number of conflicting responses was presented using either of the two possible alternate fingers. The prepotent-only blocks were included to prevent degradation of the prepotent-response representation over time, and consisted of 5 trials identical to those in the prepotent baseline condition. The data presented in the current paper were collected as part of a larger study designed to examine the effects of different types of sequences on the neurophysiological and behavioral response to conflict. However, the sequence-type effects are presented elsewhere. The current aim was to focus on age differences in the mixed condition because it was the most clear-cut in terms of conflict-processing and response-reprogramming demands.

## Data Acquisition

To synchronize EEG and kinematic measures, a key press activated a switch that sent a trigger to two data-acquisition (DAQ) computers, signaling the occurrence of a response. The response triggers were sent to the EEG-acquisition computer, and to a DAQ card (NI USB-6221 BNC; National Instruments, Inc., Austin, TX). Stimulus triggers were also sent to both the EEG-acquisition computer and the DAQ by the stimulus-presentation software (Inquisit 3.0.4.0; Millisecond Software, LLC, Seatle, WA). Movement data were recorded using a 3-D motion-capture system (VZ3000; Phoenix Technologies Inc., Burnaby, BC, Canada) that tracked the movement of light-emitting diode (LED) markers placed on each finger nail of the right hand, excluding the thumb. In order to synchronize the motion-capture data with stimuli and responses, a program was custom written in C# on Version 1.1 of the Microsoft .NET Framework. This program recorded the motion-capture frame number at the times that the stimulus and the response triggers were received by the DAQ. Stimulus and response timings were then synchronized with the motion-capture data offline using a custom written function in Matlab (Natick, MA).

The EEG-acquisition software accepted stimulus and response triggers and implanted these codes in the EEG-data stream for synchronization. A continuous EEG was recorded with an active electrode EEG system, ActiveTwo (BioSemi, Amsterdam, the Netherlands), using a 64-electrode nylon cap, sampled at 512 Hz in a DC to 104 Hz bandwidth. The EEG data were recorded relative to common mode sense and driven right leg (CMS/DRL) electrodes placed at the back of the head, to the left and right of a midline parietal-occipital electrode (POz), respectively. All EEG data were rereferenced offline to the linked earlobes, and also filtered offline for frequencies between 0.1–50 Hz. Horizontal and vertical electrooculograms (HEOG and VEOG, respectively) were recorded from electrodes placed above and below the left eye, and on the outer canthi of both eyes. These HEOG and VEOG recordings were used to monitor eye movements, and trials with HEOG activity exceeding +/−75 μV were rejected. VEOG artifacts (i.e., eyeblinks) were corrected using a spatial filter-correction technique (Method 2, Compumedics *NeuroScan Edit 4.3 Manual,* 2003). Trials with EEG activity and other motion artifacts exceeding +/–100 μV were rejected.

## Kinematic Analyses

For the current paper, the data were separated into five different response types: the random-baseline, prepotent baseline, and prepotent-only responses were analyzed to provide baseline measures of performance for each age group. Most important to note, we tested predictions about age differences in conflict processing by comparing prepotent and conflicting responses extracted from the mixed condition. All analyzed responses were defined as the second press in each pair except for the random baseline, for which all responses were included. The total number of each response type is presented in Figure 1. The motion-capture frames were used to synchronize the stimulus and response triggers with the movement data. The kinematic analysis tools were custom written in Matlab, and adapted in part from the tools developed for our previous experiments (Trewartha et al., 2009; Trewartha et al., 2011). The current data were first processed into 900 ms epochs around each stimulus, from 100 ms before the stimulus to 800 ms after the stimulus. The specific response finger was then identified as the LED marker with the maximum peak at the time of the response trigger. In the event that a response trigger was missing from an epoch, a peak detection algorithm (as described in Trewartha et al., 2009) was employed to determine if there was a key press that failed to activate the switch (i.e., was not pressed fully). Briefly, key presses were identified as local minima (i.e., troughs) among samples that were more than three standard deviations below the baseline in the vertical (z) dimension. In the event that more than one response occurred in an epoch, the first key press after the stimulus was accepted as the response. A response was considered accurate if the correct finger made a response while the stimulus was on the screen or during the ISI. Planning and execution time were calculated using the time of the full key press (i.e., trough) and the movement-initiation time. Movement initiation was defined by a backward search from the trough to the point at which the movement was below 5% maximum velocity of the key press. Planning time was defined as the elapsed time from the stimulus to movement initiation, and execution time as the time from movement initiation to full response. Only kinematic data for correct responses were included in the analyses.

## ERP Analyses

ERP analyses were conducted using Scan software (Compumedics Neuroscan, Charlotte, NC). Akin to the movement data, stimulus-locked EEG epochs of 900 ms (−100 ms to 800 ms) were obtained to assess waveform differences between various stimulus/response types. For each participant, average waveforms were computed only for trials in which there was a correct response. Averages were baseline-corrected to a 0 μV average of the 100 ms prestimulus interval. In order to explore age differences in cognitive control processes, the mean average amplitude was computed in the 300–600 ms interval after the stimulus onset (i.e., one of the boxes lighting up) to characterize the P3b component. Although the P3b typically exhibits a posteriocentral maximum (see Polich, 2007), we allowed for possible age differences in topography (Friedman, Kazmerski, & Fabiani, 1997) by comparing the average amplitude between prepotent and conflicting trials at the frontal, fronto-central, central, centro-parietal, and parietal midline sites (Fz, FCz, Cz, CPz, and Pz). The number of trials in the prepotent response average for the younger adults ranged from 152 to 237 ($M = 212.2$, $SD = 33.6$); and for the older adults from 172 to 238 ($M = 214.0$, $SD = 18.0$). For the conflicting responses, the number of trials for the younger adults ranged from 31 to 58 ($M = 46.4$, $SD = 8.8$); and for older adults from 31 to 55 ($M = 42.9$, $SD = 7.0$). The peak amplitude within the P3b interval was also recorded to compare differences in the latency of the component between the age groups.

# Results

The ANOVA designs used to make age group and response type comparisons are described separately in each section below. Whenever necessary, comparisons are reported with a Greenhouse-Geisser correction, and all tests of simple main effects are reported with IBM-SPSS Bonferroni adjusted $p$ values.

## Motion-Capture Data

The behavioral analyses provide a comparison of younger and older adults' movement patterns across the five different response types. We conducted an Age Group × Response Type (random, prepotent baseline, prepotent only, prepotent-in-mixed, and conflicting) ANOVA for each dependent variable (see Figure 2). For accuracy, there was a main effect of response type, $F(4, 27) = 6.43$, $p < .01$, $\eta^2 = 0.17$, and a significant interaction between response type and age group, $F(4, 27) = 2.83$, $p = .05$, $\eta^2 = 0.07$. Pairwise comparisons revealed that older adults were less accurate for the conflicting responses compared with the prepotent responses in the prepotent-only, $t(14) = -4.42$, $p < .01$, and prepotent-in-mixed conditions, $t(14) = -3.18$, $p < .05$, but not the other response types ($p > .55$). The younger adults performed all response types at a similar accuracy level. For planning time, there were significant main effects of age group, $F(1, 30) = 16.48$, $p < .001$, $\eta^2 = 0.36$, and response type, $F(4, 27) = 183.53$, $p < .001$, $\eta^2 = 0.85$, and a significant interaction between age group and response type, $F(4, 27) = 3.52$, $p < .05$, $\eta^2 = 0.11$. The older adults spent more time planning the random, $t(30) = 4.36$, $p < .001$, prepotent-only, $t(30) = 2.25$, $p < .05$, prepotent-in-mixed, $t(30) = 2.93$, $p < .01$, and conflicting responses, $t(30) = 5.66$, $p < .001$, compared with younger adults. However, the age groups did not differ in planning time for the prepotent-baseline condition, $p > .12$. For execution time, there was a significant interaction between response type and age group, $F(4, 27) = 4.33$, $p < .05$, $\eta^2 = 0.12$. The younger adults spent more time executing the prepotent-baseline responses than older adults, $t(30) = 2.40$, $p < .05$, but no other age group comparisons were significant ($p > .15$). Thus, older adults performed as well as younger adults in the most predictable, prepotent-baseline condition. However, relative to the younger adults, the performance of the older adults suffered on prepotent trials when conflicting responses were introduced, that is, when the groups were compared on the prepotent-in-mixed, and prepotent-only responses.

In our previous work, evidence of response reprogramming came from an observation of shorter execution time for conflicting compared with prepotent-baseline responses in younger, but not older adults (Trewartha et al., 2009; Trewartha et al., 2011). A similar pattern was observed in the current data. Critical support for the response-reprogramming interpretation of this finding was a significant negative correlation between planning time and execution time on conflicting responses in younger, but not older adults (Trewartha et al., 2009). To confirm that the same evidence for response reprogramming could be replicated in the current data, we calculated the Fisher $r$ to $z$ transformed correlations between planning and execution time for conflicting responses for each age group. This analysis revealed a negative average correlation in both younger, $M_{zr} = -0.57$ ($SD = 0.31$), and older adults, $M_{zr} = -0.38$ ($SD = 0.19$), with a significantly larger correlation for younger adults, $t(30) = -2.08$, $p < .05$. These

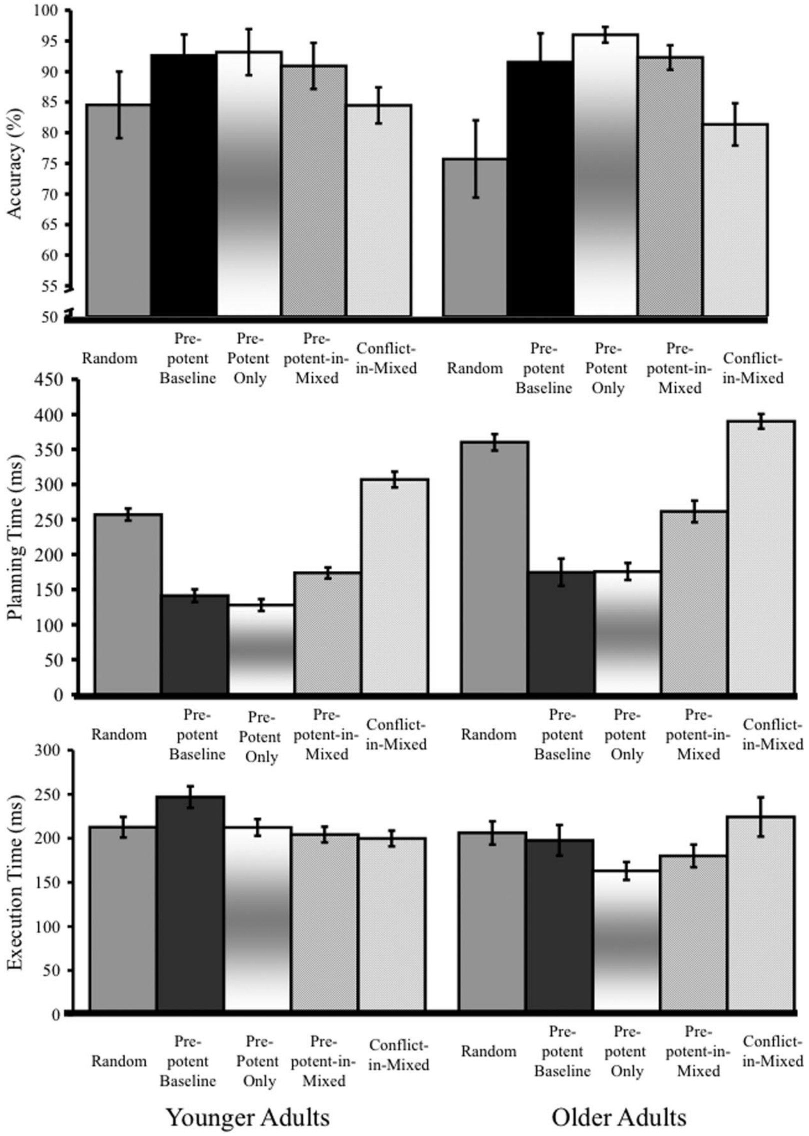


*Figure 2.* Younger and older adults' behavioral data for all conditions. Age-group averages are shown for all five response types: random, prepotent-baseline, prepotent-only, prepotent-in-mixed, and conflicting responses. The panel displays (a) averaged accuracy, (b) averaged planning time, and (c) execution time. Error bars represent standard error of the mean.

behavioral findings are robust, as they largely replicate our previous observations that older adults have more difficulty than younger adults suppressing a prepotent key press, and are less efficient at response reprogramming (Trewartha et al., 2009; Trewartha et al., 2011).

## ERP Data

We examined the ERP data to test whether context-updating processes were recruited following conflicting-stimulus presentation, and whether the recruitment of those context-updating processes differed between the age groups. To do this, we compared stimulus-locked ERP waveforms associated with conflicting stimuli, with prepotent stimuli during the conflict blocks (see Figure 3). Visual inspection of these waveforms revealed a positive deflection in the averaged waveform, peaking between 300 and 600 ms after stimulus presentation that was larger for the conflicting than prepotent stimuli for both age groups over midline sites Fz, FCz, Cz, CPz, and Pz. For both age groups, this component was maximal over posterior parietal sites consistent with classification as the P3b.[1]

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[1] Due to the nature of the stimulus presentation, early visual evoked potentials were not elicited in this experiment. Visual stimuli were dark-grey boxes that remained on the screen throughout the entire experiment. Responses were cued by a change in color of one of the boxes from dark-grey to purple; thus, there was no discrete visual stimulus onset to evoke early sensory ERPs.

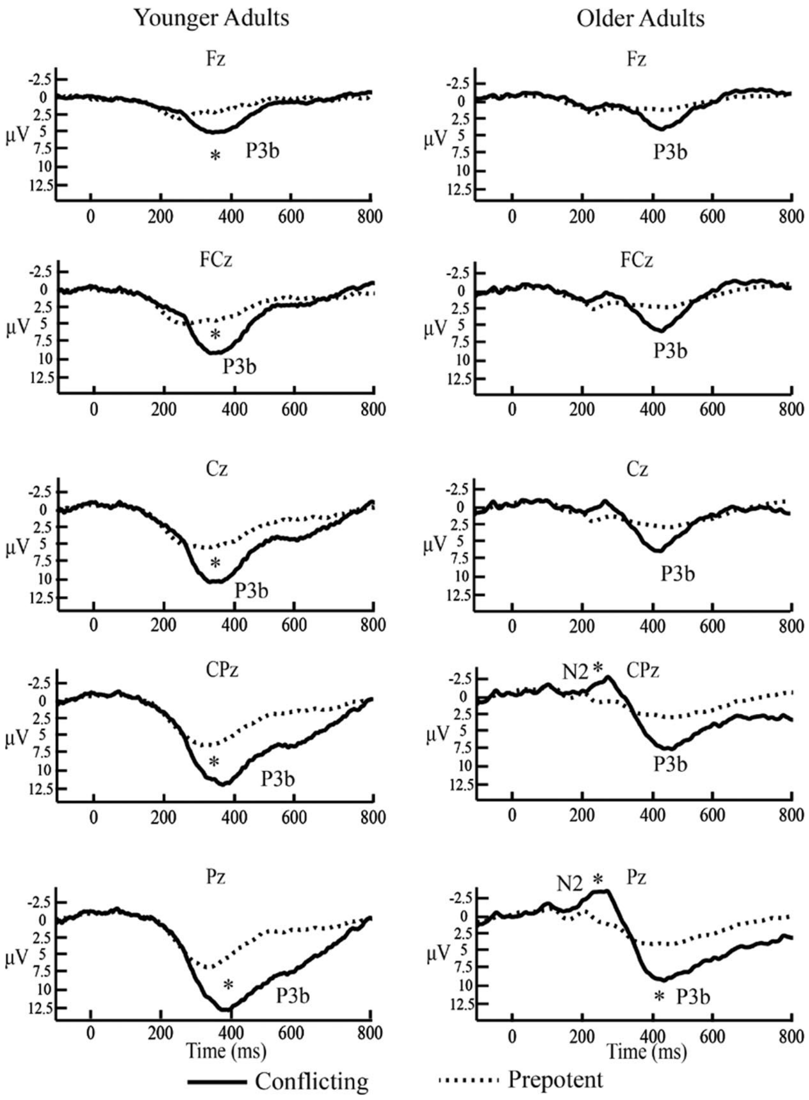

*Figure 3.* Stimulus-locked, grand-averaged ERP waveforms for younger and older adults comparing the prepotent and conflicting stimuli in the mixed blocks. The waveforms demonstrate larger P3b amplitude for conflicting, compared with prepotent, stimuli, that is greatest at posterior midline electrode sites. In addition, older, but not younger, adults, showed an N2 component preceding the P3b at posterior electrode sites. Significant differences ($p < .05$) between stimulus types in P3b and N2 amplitude are indicated with asterisks at electrode sites within each age group.

To compare the amplitude of the P3b component between the age groups (see Figure 3), we computed the averaged amplitudes in the 300–600 ms poststimulus interval and conducted an Age Group (younger vs. older) × Response Type (conflict vs. prepotent response) × Electrode Site (Fz, FCz, Cz, CPz, and Pz) ANOVA. There was a main effect of response type with a more positive amplitude for the conflicting compared with prepotent responses, $F(1, 30) = 15.5$, $p < .001$, $\eta^2 = 0.32$, a main effect of age group, with younger adults having a larger amplitude than older adults overall, $F(1, 30) = 4.23$, $p < .05$, $\eta^2 = 0.12$, and a main effect of electrode site, $F(4, 27) = 14.23$, $p < .001$, $\eta^2 = 0.28$, with greatest amplitude at Pz. There were significant interactions between age and electrode site, $F(4, 27) = 5.82$, $p < .01$, $\eta^2 = 0.12$, and between response type and electrode site, $F(4, 27) = 11.6$, $p < .001$, $\eta^2 = 0.25$. It is important to note, there was a significant three-way interaction between age group, response type, and electrode site, $F(4, 27) = 3.93$, $p < .05$, $\eta^2 = 0.09$. Pairwise comparisons revealed that for younger adults the P3b was significantly larger for conflicting than prepotent responses at all five electrode sites, Fz, $t(16) = 2.44$, $p < .05$, FCz, $t(16) = 2.39$, $p < .05$, Cz, $t(16) = 3.2$, $p < .01$, CPz, $t(16) = 4.63$, $p < .001$, and Pz, $t(16) = 6.15$, $p < .001$; however, for older adults the P3b amplitude was significantly larger for conflicting responses only at Pz, $t(14) = 2.14$, $p < .05$, but not at the other midline sites ($p > .12$). The observation of a larger P3b component following conflicting rather than prepotent responses is consistent with our hypothesis that conflict processing requires the recruitment of context-updating processes in both age groups. However, the attenuation of the P3b component in the older adult group suggests that the recruitment of context updating is diminished with age.

Aside from age differences in amplitude, inspection of Figure 3 revealed a latency shift of the P3b with aging. To explore this shift we determined the latency of the peak of the P3b for the conflicting stimulus from the average waveform for each individual. Peak latency was defined as the time of the maximum amplitude between 300 and 600 ms poststimulus. This analysis was limited to electrode site Pz, as the P3b amplitude was maximal at this site. A *t* test conducted to compare the age groups revealed that the P3b was significantly delayed in the older, compared with younger, adults, $t(30) = -2.71$, $p < .05$. This increase in latency of the P3b component in the older adult group may help explain why their planning time was longer than that of younger adults on conflicting responses. To illustrate this point, Figure 4 presents an overlay of the younger and older adults' average movement time-course data, with their grand-averaged waveforms for conflicting responses. As can be observed, the latency shift of the P3b component in the elderly coincides with their delayed movement onset relative to younger adults.

A final observation from Figure 3 is that older adults showed an N2 component immediately preceding the P3b for conflicting responses that was absent in the younger adults. To quantify the N2 component, we calculated the averaged amplitude between 150 and 300 ms poststimulus for conflicting and prepotent stimuli for each individual. To determine whether the amplitude of this N2 differed between the age groups, and whether it is related to conflict processing, we conducted an Age Group (younger vs. older) × Response Type (conflict vs. prepotent response) × Electrode Site (Fz, FCz, Cz, CPz, and Pz) ANOVA on these averages. The results revealed a significant main effect of age group, with older adults having a larger N2 than younger adults, $F(1, 30) = 9.40$, $p < .01$, $\eta^2 = 0.24$, a significant effect of electrode site, $F(4, 27) = 7.42$, $p < .001$, $\eta^2 = 0.16$, and a significant interaction between age group and electrode site, $F(4, 27) = 10.19$, $p < .01$, $\eta^2 = 0.21$. There was also a significant three-way interaction between age, response type, and electrode site $F(4, 27) = 6.18$, $p < .01$, $\eta^2 = 0.16$. Pairwise comparisons revealed that the N2 amplitude for younger adults did not differ between conflicting and prepotent responses at any electrode site ($p > .52$), whereas older adults exhibited a larger N2 for conflicting compared with prepotent responses at CPz $t(14) = 1.96$, $p = .06$, and Pz, $t(14) = 3.30$, $p < .01$.

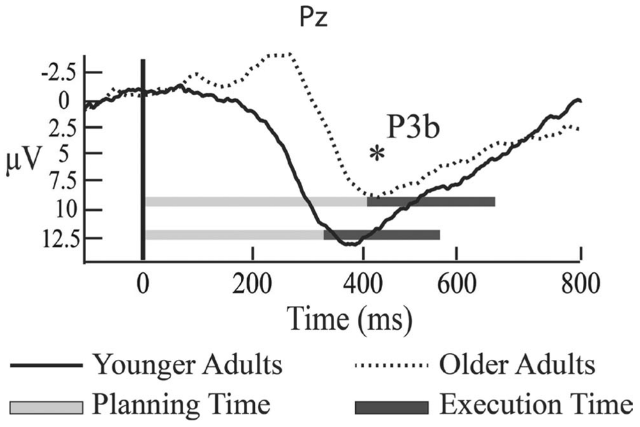

*Figure 4.* Stimulus-locked, grand-averaged ERP waveforms comparing younger and older adults on conflicting stimulus trials. The waveforms demonstrate a significant delay in latency for older, compared with younger participants in the peak of the P3b component (signified by asterisks $p < .05$). The kinematic data are superimposed on the ERP waveforms for demonstration purposes. The light gray bars represent the planning time, and the dark gray bars represent execution time. The transition between those measures denotes the average moment of movement initiation for each group. Note the general correspondence between the age-related increase in the execution time and the subsequent peak of the P3b.

It is possible that the age differences in P3b amplitude could be influenced by this group difference in the preceding N2 amplitude. To take the N2 component into account, we conducted a peak-to-peak analysis by calculating the difference between the N2 and P3b peak amplitudes. The peak of the N2 was defined as the minimum value between 150 and 300 ms, and the peak of the P3b was scored as the maximum value between 300 and 600 ms poststimulus. This alternative measure was subjected to an Electrode Site (Fz, FCz, Cz, CPz, and Pz) × Age Group (younger vs. older adults) ANOVA. The results showed a significant main effect of electrode site, $F(4, 27) = 59.24$, $p < .001$, $\eta^2 = 0.65$, such that the magnitude of the N2–P3b complex was largest at posterior sites. Although the amplitude was also larger for younger adults ($M = 12.79$, $SE = 1.22$) than older adults ($M = 10.8$, $SE = 1.34$), this difference was not significant ($p = .28$).

To summarize, younger and older adults exhibited a large P3b component for conflicting, but not prepotent stimuli that was maximal over posterior midline electrode sites, consistent with the P3b component. The amplitude of this P3b component was attenuated, with a delayed peak in the older compared with younger adults. In addition, the P3b for conflicting stimuli was preceded by an N2 component at posterior electrode sites in the older, but not younger adults.

## Combined Motion-Capture and ERP Data

The finding of a robust P3b component following conflicting stimuli is consistent with the idea that processing conflicting stimulus information requires the recruitment of context-updating processes. However, it is important to also investigate how these updating processes impact the successful reprogramming of the conflicting response. To test the hypothesis that context updating plays a role in response reprogramming, and that the P3b component is related to flexible movement adaptation during conflicting responses, we compared P3b amplitude for faster and slower conflicting responses within each individual. To do this we found the median execution time for all conflicting responses for each individual. For younger adults, faster conflicting responses had a mean planning time of $M = 319.33$ ms ($SD = 43.31$) and mean execution time of $M = 155.94$ ms ($SD = 26.96$), whereas slower responses had a mean planning time of $M = 296.69$ ms ($SD = 48.92$) and mean execution time of $M = 238.39$ ms ($SD = 49.48$). For older adults, faster conflicting responses had a mean planning time of $M = 406.20$ ms ($SD = 86.21$) and mean execution time of $M = 158.51$ ms ($SD = 43.69$), whereas slower responses had a mean planning time of $M = 344.94$ ms ($SD = 37.10$) and mean execution time of $M = 285.04$ ms ($SD = 140.63$). We compared the averaged amplitude of the P3b for conflicting responses that were faster, and slower than the median in an Age Group (younger vs. older) × Execution Speed (faster or slower than the median) × Electrode Site (Fz, FCz, Cz, CPz, and Pz) ANOVA (see Figure 5). It is important to note that this analysis revealed a significant interaction between age group and execution speed, $F(1, 30) = 4.12$, $p = .05$, $\eta^2 = 0.12$, such that the P3b was significantly larger for conflicting responses that were faster compared with slower than the median execution time for younger, $t(16) = 2.45$, $p < .05$, but not older adults. From Figure 5, it appears that this effect in the younger adults was largely driven by differences between the responses at Cz, and CPz. For older adults, there was no difference in P3b amplitude between responses with fast or slow execution time ($p > .6$). Thus, the size of the P3b component was related to shorter execution time only for younger adults.

## Discussion

The current experiment combined kinematic and ERP analyses to determine if response reprogramming is facilitated by context-updating processes, and whether age-related differences in prepotent-response suppression are related to declines in context updating that prevent successful response reprogramming. Kinematic data showed that both younger and older adults took more time to plan conflicting rather than prepotent responses, and older adults were also less accurate. In the ERP data, comparison of conflict and prepotent trials revealed a P3b component peaking

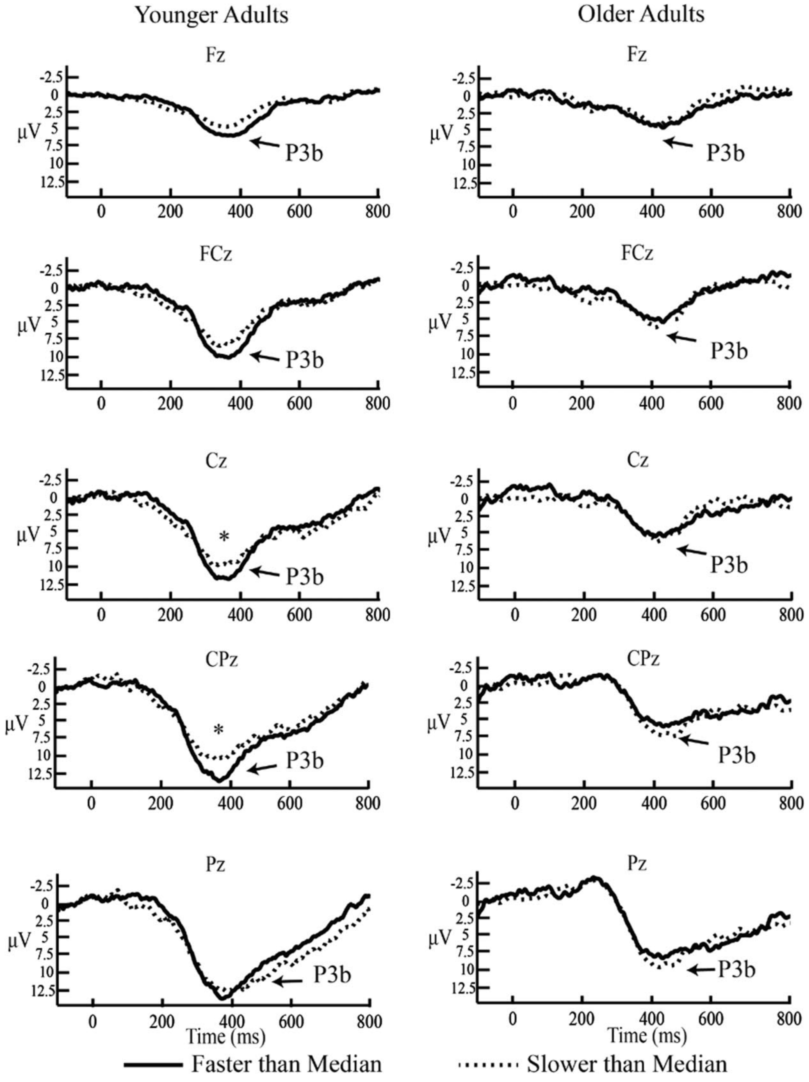

*Figure 5.* Stimulus-locked, grand-averaged waveforms are presented for younger and older adults, comparing trials that were faster (solid line) and slower (dotted line) than each participant's median execution time for the conflicting stimuli. This figure demonstrates that the amplitude of the P3b was larger for conflicting responses that were faster than the participant's median execution time for younger, but not older, adults. Significant differences ($p < .05$) are highlighted with asterisks.

between 300 and 600 ms poststimulus for both age groups that was maximal over centro-parietal electrode sites. Older adults showed reduced amplitude and a delayed peak of the P3b, but also a larger, preceding N2 component, relative to younger adults. Most importantly, we showed that for younger, but not older adults, the P3b was larger for trials with faster execution times, suggesting that better context updating led to more efficient response reprogramming. These findings are novel in showing that context updating is directly associated with adjustments in response execution, and that older adults were less able to use these context-updating processes to support successful movement reprogramming.

The current behavioral findings largely replicate our previous work, which showed that younger and older adults performed equally well for prepotent responses, but that younger adults were able to shorten movement-execution time on conflicting responses, leading to better performance than older adults (Trewartha et al., 2009; 2011). We have interpreted this shortening of execution time by younger adults as response reprogramming that facilitates execution of the conflicting responses, thereby minimizing overall RT. This interpretation is supported by a negative correlation between planning and execution time for conflicting responses that is larger in younger than older adults. In the past, we have speculated that less efficient reprogramming by older adults might be related to age-related declines in conflict monitoring that prevent them from flexibly modulating movement execution. However, as described below, the current ERP data are more consistent with an interpretation based on age-related declines in context-updating processes, leading to less flexible movement reprogramming.

## Context Updating and the P3b

In our task, the first stimulus, and/or response from the prepotent pair primes a working-memory representation and motor program. Upon encountering an unexpected conflicting stimulus, participants have to update working memory with the new response representation. The ERP data demonstrated that younger and older adults exhibited a P3b component that was larger following conflicting, compared with prepotent, stimuli. This component has been frequently associated with updating task-relevant context information in working memory (see Polich, 2007). Our results also show that the amplitude of the P3b was attenuated in the elderly and we interpret this finding as a deficiency in context updating in the older participants. The peak latency of the P3b was also delayed in the elderly, which is a ubiquitous finding in the literature. These findings are consistent with previous observations of age-related changes in the P3b component (see also Friedman, Kazmerski, & Fabiani, 1997; Polich, 1996; Polich, 1997) and with reports of diminished context updating in later adulthood (e.g., Braver & Barch, 2002; Braver, Satpute, Rush, Racine, & Barch, 2005; Braver & West, 2008). However, it should be noted that the age-related difference in P3b amplitude in the current data was reduced if the amplitude was calculated using a peak-to-peak, N2–P3 complex analysis. Thus, the overall age-related attenuation in P3b amplitude should be interpreted with caution, as it may reflect the recruitment of additional or alternative cognitive processes in the older participants.

We also note that the P3b component is known to vary inversely with stimulus probability, such that less probable stimuli lead to larger P3b amplitudes (e.g., Duncan-Johnson & Donchin, 1977; Johnson & Donchin, 1982; Squires, Wickens, Squires, & Donchin, 1976). In the current task, the conflicting responses were inherently less probable than the prepotent responses. With our design, we cannot rule out the potential contribution of stimulus-probability effects to the size of the P3b component. In spite of the stimulus-probability concern, the median-split analysis demonstrated that the amplitude of the P3b in the younger adults varied as a function of the speed with which the conflicting responses were executed. This finding shows that the size of the P3b is at least partly determined by processes associated with conflict resolution and response reprogramming. However, this finding was only observed for the younger adults. In fact, neither the N2 nor P3b varied with execution speed in the older adults. Thus, the current data support the proposal that inefficient context updating contributes to poorer performance by older adults on conflict tasks, regardless of recruitment of additional cognitive processes.

It is worth pointing out that older adults did perform the conflicting responses at a reasonably high accuracy level (approximately 80%). This observation, along with the large N2 component preceding the P3b in the older but not younger group, supports the idea that the older adults are recruiting additional cognitive processes to perform conflicting responses. Although the anterior N2–P3 complex has been commonly associated with conflict monitoring and inhibition (e.g., Randall & Smith, 2011; Smith, 2011; Yeung, Botvinick, & Cohen, 2004), the more posterior N2 component has been associated with aspects of visual attention to novel stimuli (Folstein & van Petten, 2008; Suwazono, Muchado, & Knight, 2000). A visual attention explanation is more consistent with the current data because of the topography of the N2 exhibited by older adults, and because the conflicting stimuli occur infrequently in our paradigm. This suggests that older adults are shifting their attention to the conflicting stimuli, but are less able to recruit cognitive control processes that would support efficient production of the conflicting responses. Thus, older adults may respond more slowly to the conflicts because of inefficient context-updating processes, but they may compensate by shifting attention to the conflicting stimuli in order to respond at a reasonably high level of accuracy.

## Cognitive Control, Context Updating, and Aging

The present findings are important for current theories of cognitive control implementation in aging, such as the “dual mechanisms of control” account (Braver, Gray, & Burgess, 2007). This model proposes that cognitive control is achieved through either a proactive or reactive mechanism: Proactive control allows for active maintenance of response representations such that individuals can anticipate upcoming responses; the reactive mechanism deploys cognitive control only after a stimulus has been presented. When a conflicting stimulus is unexpected, reactive control is likely recruited to aid response production. It has been argued that older adults are less able to utilize proactive control, and instead rely more on reactive control, which is thought to be better preserved in the elderly (e.g., Braver et al., 2007). The current data, in addition to our previous findings (Trewartha et al., 2011), are consistent with an age-related decline in proactive control. The older adults performed prepotent responses as well as younger adults when they were presented in isolation in the prepotent-baseline condition. However, after the conflicting responses were introduced, the older adults performed prepotent responses more poorly in the prepotent-only and conflicting conditions. This finding is consistent with previous research showing that older adults exhibit a decline in context activation/updating, but not in context maintenance (Braver et al., 2005), and that older adults experience a decline in the ability to manage competing mental sets (e.g., Mayr & Liebscher, 2001).

The current observation of a large P3b component following conflicting, but not prepotent, stimuli is consistent with the recruitment of reactive control for updating working memory during conflict processing. However, reactive control may be less effective in the elderly, as older adults were less accurate than younger adults on conflicting responses, and exhibited an attenuated and delayed P3b component. This claim is further strengthened by the lack of modulation of P3b amplitude with execution speed in the older adults. These findings are consistent with other observations of age-related reductions in the amplitude of stimulus-locked, conflict-related ERP components (e.g., Falkenstein et al., 2002; Mager et al., 2007; West, 2004), and with previous suggestions that reactive control is less efficient in older than in younger adults (e.g., Braver et al., 2005).

## The Role of Context Updating in Response Reprogramming

The reason for these age differences in reactive control efficiency may lie in the transition between processing stimulus identity and preparing appropriate actions. The dual mechanisms of control account proposes that reactive control can rapidly influence response output through updating of working memory (Braver et al., 2007). However, the mechanism by which cognitive control influences response execution has not been previously examined. The dominant historical view of the P3b in terms of context updating was that it represents memory updating of information related to stimulus identity/evaluation, independent of response-related processes (Donchin, 1981; Donchin & Coles, 1988). More recently, it has been suggested that the P3b reflects a mediating function between stimulus processing and response preparation (e.g., Verleger et al., 2005). One mechanism by which the updating of task-context information could influence response preparation in conflict tasks is through response reprogramming (e.g., Bellgrove et al., 1998; Mars et al., 2007; Neubert et al., 2011). Indeed, recent research has demonstrated an important role for general working-memory mechanisms in response replanning and execution (Spiegel, Koester, & Schack, 2013).

In the current task, response reprogramming is operationalized by a shortening of execution time during conflicting compared with prepotent responses, and by a negative correlation between planning and execution time for conflicting responses. If context-updating processes associated with the P3b allow for successful response reprogramming, then responses with faster execution time should be associated with a larger P3b response. The current younger adult data provide clear support for this prediction. When execution time on the conflicting responses was faster than the median, the P3b component was larger than trials in which execution time was slower than the median. Put another way, on trials in which younger adults updated working memory more effectively, their conflicting responses were executed more rapidly. This finding demonstrates that, at least for younger adults, response reprogramming is facilitated by the updating of working memory with information about the unexpected conflicting response. Thus, response reprogramming may be a viable mechanism by which reactive control influences task performance, through context updating, in the type of short time scale proposed by Braver et al. (2007).

In this context, it is important to reiterate that reactive control may not be as efficient in the elderly as in younger adults. The older adults did not shorten execution time for conflicting compared with prepotent responses, and they exhibited a smaller correlation between planning and execution time for the conflicting responses. The net effect of these two factors is a disproportionately longer RT for conflicting responses in older than in younger adults. These behavioral findings are extended by the ERP results showing that the older adults did not exhibit the same modulation of the P3b as a function of movement-execution speed. Thus, the current data add to existing evidence of age-related declines in context updating (e.g., Braver et al., 2005) by demonstrating a consequence of less efficient context updating to movement reprogramming. Specifically, the overall speed with which older adults perform conflicting responses may be reduced in part because less efficient context-updating processes prevent successful movement reprogramming.

## Neural Basis of Response Reprogramming

Although the current data support the idea that context updating can facilitate response reprogramming, the neural mechanisms through which this occurs are not well understood. In part, this is because researchers do not yet agree on the neural basis of the P3b component. For the context-updating process to influence response reprogramming, the anatomical substrates of those processes should communicate with areas known to be involved in movement preparation/reprogramming. The parietal P3b has been previously linked to the hippocampus (e.g., Halgren et al., 1980), but more recently, research has demonstrated a crucial role of the temporal-parietal junction (e.g., Verleger, Heide, Butt, & Kömpf, 1994). This is consistent with observations that a fronto-parietal network of brain areas supports working memory function (e.g., Klingberg, O'Sullivan, & Roland, 1997; Owen, McMillan, Laird, & Bullmore, 2005). Indeed, current theories of the P3b suggest that it is part of a circuit between frontal- and temporal-parietal areas that functions to support context updating (see Polich, 2007). This circuit may also represent the basis for a connection between context-updating and response-reprogramming processes.

The regions thought to be involved in response reprogramming include the presupplementary motor area (pre-SMA), right inferior frontal cortex (rIFC), the subthalamic nucleus (STN), and the primary motor cortex (M1). The pre-SMA in particular has been shown to be responsible for response reprogramming during response conflict (e.g., Isoda & Hikosaka, 2007; Mars et al., 2009) and likely contributes to the development of the motor program that is used by M1 to execute the desired response (e.g., Humberstone et al., 1997; Ikeda et al., 1999; Isoda & Hikosaka, 2007). In fact, it has been proposed that this network exerts its influence by inhibiting or facilitating M1, depending on task demands (e.g., Neubert et al., 2011). For example, in the stop-signal paradigm, this fronto-basal ganglia network has been implicated in response inhibition (e.g., Aron et al., 2007). Our P3b data are consistent with the recruitment of response-reprogramming and context-updating processes that have been attributed to this fronto-temporal-parietal network. Future research investigating the activation of these networks during conflict tasks would further strengthen the theory that context-updating processes facilitate response reprogramming.

In summary, our study has revealed that the performance of conflicting responses is facilitated by response reprogramming in younger adults, as evidenced by shortened execution time relative to prepotent responses. Modulation of the P3b component as a function of response-execution speed in younger adults suggests that response reprogramming is facilitated by context-updating processes. The lack of P3b modulation with execution speed in the elderly suggests that declines in prepotent response suppression are related to the extent to which older adults update working memory with relevant task-context information.

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