# The Cerebellum Mediates Conflict Resolution

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## Abstract

■ Regions within the frontal and parietal cortex have been implicated as important neural correlates for cognitive control during conflict resolution. Despite the extensive reciprocal connectivity between the cerebellum and these putatively critical cortical areas, a role for the cerebellum in conflict resolution has never been identified. We used a task-switching paradigm that separates processes related to task-set switching and the management of response conflict independent of motor processing. Eleven patients with chronic, focal lesions to the cerebellum and 11 healthy controls were compared. Patients were slower and less accurate in conditions involving conflict resolution. In the absence of response conflict, however, task-switching abilities were not impaired in our patients. The cerebellum may play an important role in coordinating with other areas of cortex to modulate active response states. These results are the first demonstration of impaired conflict resolution following cerebellar lesions in the presence of an intact prefrontal cortex. ■

## INTRODUCTION

A hallmark of human attentional functions is cognitive control. Animal and human studies have converged to highlight a network of structures within the frontal lobes responsible for cognitive and behavioral control (e.g., O'Reilly, Noelle, Braver, & Cohen, 2002; Stuss & Levine, 2002; Birrell & Brown, 2000; Stuss & Alexander, 2000; Dias, Robbins, & Roberts, 1996). Cognitive control is particularly important during situations of response conflict, such as when multiple competing responses are activated, when responses are not uniquely mapped to stimuli, or when the suppression of prepotent responses is required. This conflict resolution has been related primarily to the anterior cingulate cortex and the dorsolateral prefrontal cortex (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999). Although the cerebellum has been implicated in attentional functions (Schmahmann & Sherman, 1998; Courchesne et al., 1994; Akshoomoff & Courchesne, 1992; Fiez, Petersen, Cheney, & Raichle, 1992; Grafman et al., 1992), and is densely connected to the prefrontal cortex (PFC) (Allen et al., 2005; Middleton & Strick, 2001; Schmahmann, 2001), a potential role for the cerebellum in conflict resolution has yet to be identified.

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The task-switching paradigm (see Monsell, 2003, for review) involves a high degree of cognitive control and often requires conflict resolution in addition to task-set switching. Although an investigation of response conflict in task switching has never been implemented in an adult population of patients with focal cerebellar lesions (see Berger et al., 2005, for a study with children), imaging studies investigating areas of activation during task switching have implicated the cerebellum as an important neural correlate (Barrett et al., 2003; Dreher, Koechlin, Ali, & Grafman, 2002; Le, Pardo, & Hu, 1998). To our knowledge, none of this research has specifically addressed conflict resolution during task-set switching.

In the present study, we used a variant of a paradigm developed by Meiran (1996) in which task-switching demands and the difficulty of resolving response conflict were manipulated orthogonally. Each stimulus is mapped to two classifications, one in each task. For half of the stimuli, each classification maps to a different response (incongruent trials) and, for the other half, each classification maps to the same response (congruent trials). Thus, with this arrangement, four possible pairings of task switching and response difficulty are possible: response conflict at the level of response selection without task-set switching (incongruent, task repetition trials), task-set switching without response conflict (congruent, task switch trials), response conflict with task-set switching (incongruent, task switch trials), and neither response conflict nor task-set switching (congruent, task repetition trials). The advantage of this design is that task switching and conflict resolution can be measured independently using the same experimental tool.

Sudevan and Taylor (1987) were the first to demonstrate the effects of congruency in the context of a task-switching paradigm. In this experiment, participants switched between classifying a single digit as either ODD or EVEN and HIGH (greater than 5) or LOW (less than 5). With these criteria there could be congruent trials (e.g., ''9'' which is both HIGH and ODD) in which the correct keypress was the same in both tasks, and incongruent trials (e.g., ''1'' which is LOW and ODD), in which the correct keypress was different in the two tasks. Importantly, Sudevan and Taylor reported that performance on the congruent trials was faster than on the incongruent trials. Although these findings were derived from non-brain-damaged participants, there are several studies on lesions and special populations which suggest a link between congruency effects and the PFC. Specifically, Aron, Monsell, Sahakian, and Robbins (2004) as well as Keele and Rafal (2000) found that lesions to the PFC were associated with poorer performance on incongruent trials. Stoet and Snyder (2003) found that monkeys, whose PFC is proportionally much smaller than in humans, had increased congruency effects relative to humans. Additional evidence comes from human populations where PFC functioning is believed to be compromised, such as in young children (Cepeda, Kramer, & Gonzalez de Sather, 2001) and in the elderly (Meiran, Gotler, & Perlman, 2001).

If the cerebellum is important for resolving conflict prior to response preparation proper, patients with focal cerebellar lesions should experience more difficulty on incongruent trials than controls, leading to slower response times (RTs) and/or reduced accuracy, regardless of whether the task switches or repeats from the preceding trial. If the cerebellum is important for task-set switching, impairment should be observed following task switches, regardless of whether the stimulus evokes response conflict.

## METHODS

### Participants

Eleven patients (age range = 24–74 years, mean = 53.3 years; education range = 7–21 years, mean = 12.8 years) with focal cerebellar lesions were tested at least 90 days postinjury (range = 90–1035; mean = 510.8). Etiology of injury was restricted to vascular (6) and benign tumor excision (5). The patient demographics are presented in Table 1. Lateralization of lesions was right (5), left (5), and bilateral (1). Structural MRI (all patients received 1.5-T MRI scans), examined by an experienced neurologist (MPA), confirmed no evidence of extracerebellar damage. Lesions were reconstructed using a cerebellar template developed by Ivry and colleagues and were shown in Figure 1. None of the patients had a previous stroke, traumatic brain injury, any other neurological disease, or any axis-I *DSM* diagnosis. Eleven healthy adults without neurological or psychiatric disorder (age range = 28–77 years; mean = 54.3 years; education range = 11–20 years, mean = 15.1 years) matched for age ($t = 0.17$, *ns*) and education level ($t = 1.69$, *ns*) to the patients were also tested. All participants had normal or corrected-to-normal vision and color perception. All participants provided written informed consent prior to commencing the experiment according to the Declaration of Helsinki. Ethical approval for this research was obtained by the Toronto Academic Health Sciences Council.

### Apparatus and Stimuli

All stimuli were displayed by IBM-compatible PCs on color monitors. Stimuli were mid-gray and presented on a black background. Following the procedure described by Meiran (1996), a 2 × 2 grid was displayed at screen center, subtending 2.2° × 2.2° of visual angle when

**Table 1.** Patient Information

| Patient | Sex | Age | Education | Etiology | Time Post Injury (days) |
| --- | --- | --- | --- | --- | --- |
| 1 | M | 74 | 14 | Vascular | 260 |
| 2 | M | 70 | 18 | Benign tumor | 377 |
| 3 | F | 65 | 7 | Vascular | 328 |
| 4 | M | 40 | 21 | Vascular | 90 |
| 5 | F | 53 | 12 | Benign tumor | 472 |
| 6 | M | 30 | 12 | Vascular | 980 |
| 7 | M | 41 | 12 | Benign tumor | 443 |
| 8 | F | 62 | 12 | Vascular | 1035 |
| 9 | M | 54 | 10 | Vascular | 842 |
| 10 | M | 59 | 8 | Benign tumor | 674 |
| 11 | F | 24 | 15 | Benign tumor | 118 |

**Figure 1.** Schematic reconstruction of the cerebellar lesions (in dark gray; light gray area represents secondary atrophy after tumor resection). In each column, sections are arranged from superior (top) to inferior (bottom) for each patient. Cerebellar templates were provided by Ivry and colleagues, University of California, Berkeley.
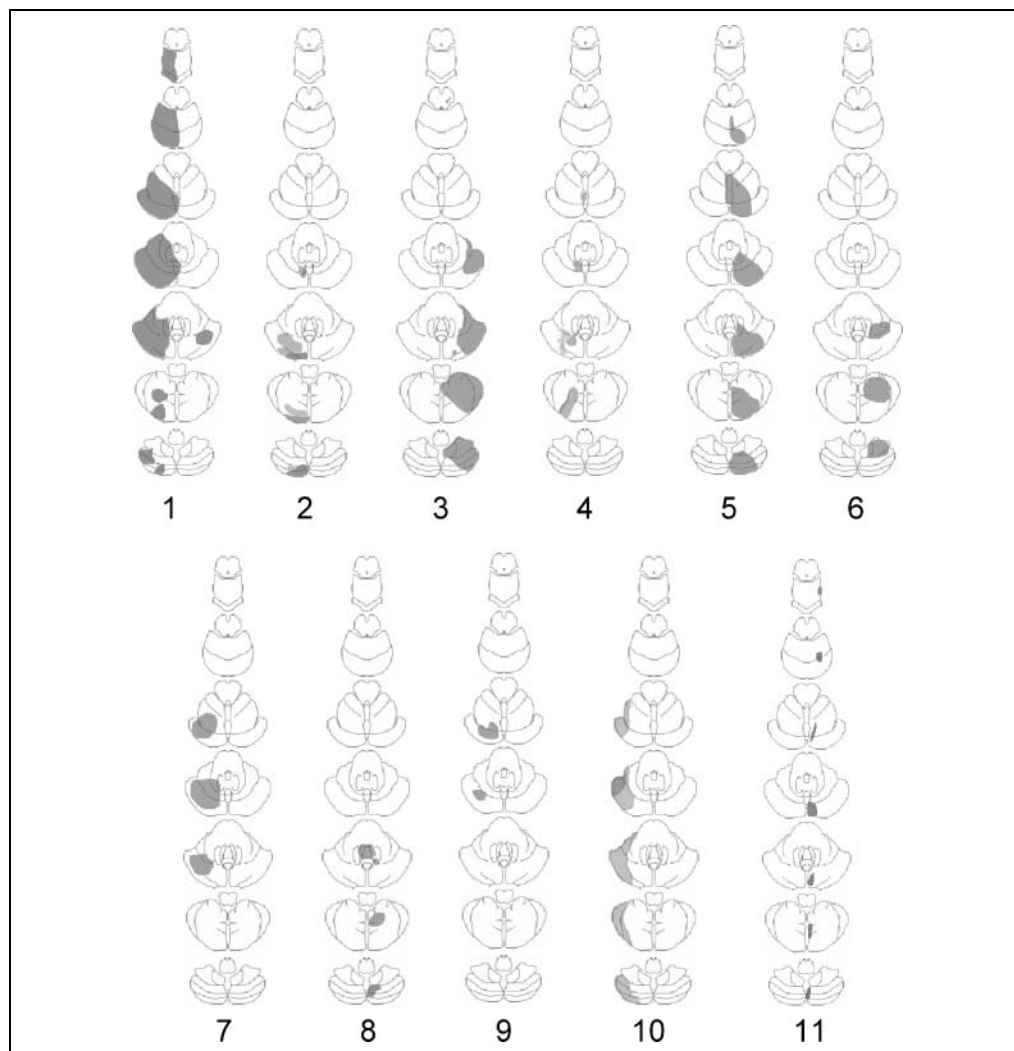


viewed from a distance of 60 cm. The target (a small star) appeared in the center of one of the four 1.1° × 1.1° quadrants of the grid, and measured approximately 0.7° × 0.7° of visual angle. Subjects indicated in which half of the grid the target appeared (top or bottom half if arrowheads appeared above and below grid; left or right half if they appeared to left and right of grid). The target was displayed with equal probability in one of the four quadrants and remained visible until response; the grid was visible at all times. Participants were required to make speeded responses with their right hand using two keys of the numeric keypad. Response-level competition was implemented between a task-relevant and a task-irrelevant stimulus attribute by mapping two stimulus locations to the same response key (congruent stimulus–response mapping) or to different keys (incongruent stimulus–response mapping; Figure 2). Larger congruency effects (incongruent RT − congruent RT) indicate greater difficulty in resolving response conflict.

## Procedure

MEL software (Schneider, 1988) was used to display stimuli and record responses. Each block began with a message instructing participants to press "b" on the keyboard when ready to proceed with the block of trials. Clearing away this message initiated the first trial, which began with the appearance of the grid. The grid was displayed by itself for one of three durations, corresponding to the response–cue interval (RCI) for the trial. With equal probability, the RCI was 200, 1500, or 3000 msec. The RCI terminated with the presentation of the task cue, displayed concurrently with the grid. The grid and task cue were presented together for a duration equal to one of three cue–target intervals (CTIs; 200, 1500, or 3000 msec), selected with equal probability. The CTI terminated with the presentation of the target for the trial, displayed with equal probability in one of four quadrants. The location of the target was chosen randomly on each trial, with the restriction that each location was chosen nine times within each block

**Figure 2.** Sequence of trial events in our task-switching paradigm. (Left) Congruent trials. Irrespective of the classification task, the response for this stimulus is congruent for participants with the key mapping shown. (Right) Incongruent trials. The upper/left key is the correct response for this stimulus when the task is to indicate whether it is in the upper or lower half of the grid. However, for the left/right classification task, the stimulus maps to a different response.



congruent trials                    incongruent trials
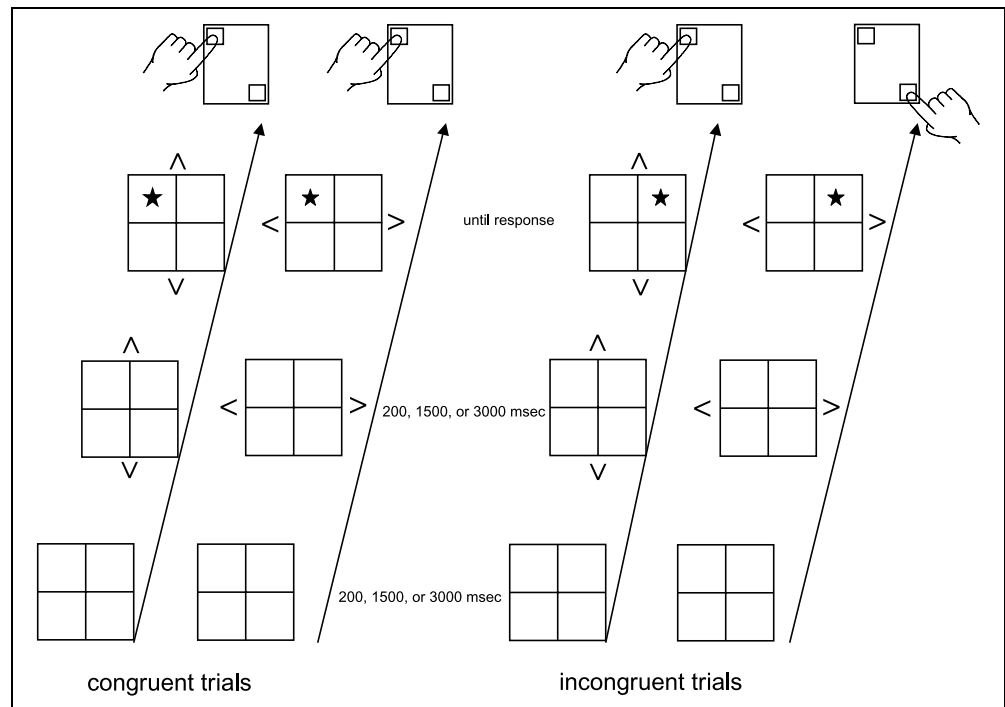
of 36 trials. Responding cleared the target, leaving only the grid and initiating the RCI for the next trial. Thus, there were no breaks between trials. Rather, subjects were instructed to rest between blocks and were explicitly reminded to do so after the 5th and 11th blocks of the experiment. Each RCI–CTI trial type was presented twice in two randomly chosen trials within each block of trials, yielding a total of 36 trials per block.

The experiment began with two blocks of practice trials and continued with 16 blocks of experimental trials. The CTI and RCI were each fixed at 1500 msec for the first block for all participants to familiarize them with the procedure. Participants responded using two keys of the numeric keypad with the key combination counterbalanced across participants. They used either the lower-right ("3") and upper-left ("7") keys, indicating DOWN and RIGHT or UP and LEFT, respectively, or the lower-left ("1") and upper-right ("9") keys to indicate DOWN and LEFT or UP and RIGHT, respectively. In order to investigate the effect of cerebellar damage on resolving response-level competition, we implemented competition between a task-relevant and a task-irrelevant stimulus attribute in the following manner. For even-numbered participants, the responses "right" and "bottom" (corresponding to the half of the grid in which the target appeared) were mapped to the "3" key (lower right), whereas the responses "left" and "top" were mapped to the "7" key (upper-left). For odd-numbered participants, the responses "left" and "down" were mapped to the "1" key, positioned at the lower left corner of the number pad, whereas the responses "right" and "top" were mapped to the "9" key (upper-right corner). Because of this arrangement, the two possible classifications for any given

target could be mapped congruently (i.e., both classifications mapped to the same key) or incongruently (each possible classification mapped to a different key). For example, for a subject with the response keys "3" and "7," a target in the upper left quadrant would be a congruent target because the response "7" would be correct in either the upper/lower judgment task or the left/right judgment task. A target in the upper right quadrant, in contrast, would be an incongruent target because the response "7" would be correct for the upper/lower judgment task but not for the left/right task (for which the correct response would be "3"). With this arrangement, response conflict would arise for incongruently mapped targets, but not for congruently mapped targets, because the task-relevant and task-irrelevant stimulus attributes map to competing responses for incongruent targets, to the same response for congruent targets. Participants were instructed to make their responses as quickly and accurately as possible. No feedback was provided.

### Design

The within-participants independent variables were RCI (200, 1500, and 3000 msec), CTI (200, 1500, and 3000 msec), switch (task switch vs. repetition), and congruency (congruent vs. incongruent). Group (patients vs. controls) was a between-participants variable.

### RESULTS

Each condition in the design was represented by its mean RT and proportion of errors (PE). These values were

analyzed in a mixed-model 2 (group) × 2 (switch) × 2 (congruency) × 3 (RCI) × 3 (CTI) analysis of variance according to the design above. The manipulation of RCI and CTI did not interact with congruency and these factors will not be reported in the following results. This finding with our patients is in line with previous results in healthy participants (Meiran, 2000; Meiran, Chorev, & Sapir, 2000).

### Response Times

Data from one patient were excluded from the analysis of RTs because his mean RTs in many cells of the design were more than three standard deviations longer than those of the other participants. Analyses were carried out both including and excluding stimulus location repetitions; because their exclusion made no difference to the outcome of the analyses, the results are reported with stimulus repetitions included. The most prominent feature of the response-time analysis was a reliable effect of congruency [$F(1, 19) = 34.1$, $MSE = 36,702$, $p < .001$], that interacted with other factors. The effect of congruency (incongruent RT − congruent RT) was considerably larger in the patients (111 msec) than in the controls (51 msec), leading to a significant Group × Congruency interaction [$F(1, 19) = 4.63$, $MSE = 36,702$, $p < .05$]. Importantly, this reliable difference in the size of the congruency effect was observed in the presence of a much larger task-switch cost that did not differ significantly between the two groups [$F(1, 19) = .003$, $MSE = 87,948$, $p > .95$]. This suggests that the difference in the size of the congruency effect cannot be attributed to a generalized deficit in cognitive processing in the patients.

The effect of congruency was much larger following a task switch in the patients (an increase of 49 msec) than in the controls (4 msec), although the Group × Congruency × Switch interaction did not reach significance [$F(1, 19) = 3.40$, $MSE = 6940$, $p < .09$; see Figure 3]. A significant Switch × Congruency interaction was observed in the patients only [$F(1, 9) = 7.39$, $MSE = 7338$, $p < .03$]. This interaction reflects the fact that the effect of congruency was greater following a task switch than following a task repetition in the patients.

### Errors

Data from all subjects were included in this analysis. The analysis was carried out both including and excluding the patient we excluded from the RT analysis. The outcome of the analysis was virtually unaffected when this patient was excluded, with the exception that the reduction in noise increased the sensitivity of the analysis of variance in detecting additional effects. As can be immediately seen in Figure 3, accuracy on the task was very high overall and, for control participants, errors were quite rare. The effect of congruency was larger following a task switch than following a task repetition, but this pattern was observed only for the patients. This led to a significant Group × Switch × Congruency interaction [$F(1, 20) = 18.9$, $MSE = 0.004$, $p < .001$]. As with RTs, the effect of task switching was much greater in the controls than the effect of congruency; the fact that patients were much more strongly affected by the congruency manipulation than controls suggests, then, that the patients are experiencing difficulty with the less demanding process. Given the small number of errors in the congruent condition, we did not interpret any other higher-order interactions in these analyses.

## DISCUSSION

These results are the first observation that the cerebellum mediates response conflict, but not task switching, an impairment which cannot be explained by any purely motor dysfunction. In fact, our patients' RTs were faster
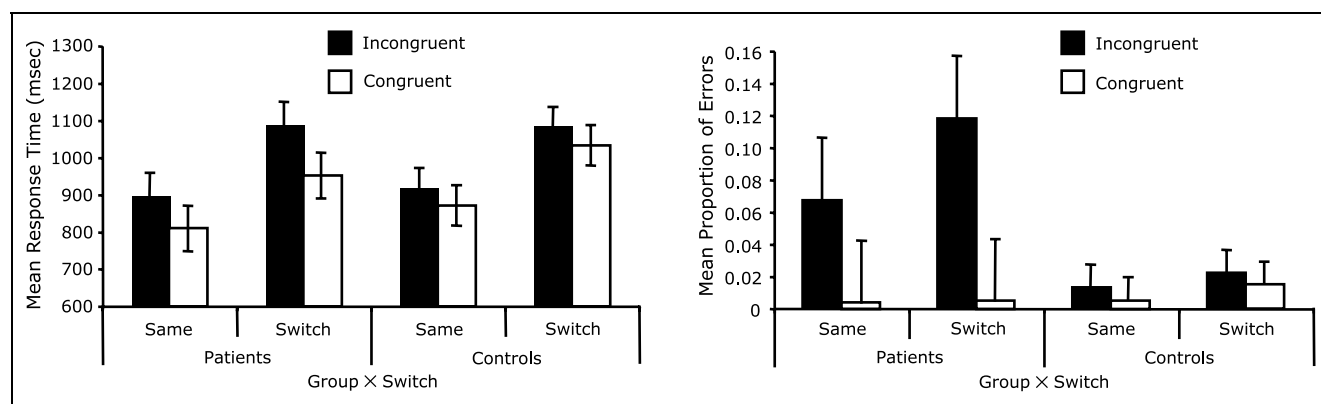


**Figure 3.** (Left) The congruency effect in RT (incongruent RT − congruent RT) during task repetition and task switch trials for patients and controls. (Right) The proportion of errors for patients and controls on congruent and incongruent trials requiring a task repetition or a task switch. Error bars represent 95% confidence intervals (Loftus & Masson, 1994).

overall, especially on congruent trials and both the patients and controls correctly categorized the target with near-perfect accuracy when the targets were congruent; this was true whether the task repeated or switched. Nevertheless, the trend found among our patients shows that resolving conflict was more difficult for them after switching tasks.

## What Type of Response Conflict is Involved?

Although it is widely agreed that congruency effects reflect some form of conflict resolution process, the exact locus of the conflict is still debated. Specifically, the conflict could be between conflicting task sets (Vertical vs. Horizontal rules, in our paradigm). Alternatively, the conflict could be between competing responses or between specific stimulus–response (S–R) rules (the mapping of two classifications to a single response key, in our paradigm). Although the locus of the conflict is immaterial for our main conclusion, identification of the source of the interference could allow for more precise specification of the cerebellum's role in conflict resolution, and in S–R assignment more generally.

We argue that the bulk of the evidence supports the notion that the conflict takes place between task rules and not between specific S–R rules or between specific responses. First, neurologically intact young adults show larger congruency effects in errors after a task switch; these effects are reduced with advance task preparation based entirely on the identity of the task set, and the pattern of results is explained well by a mathematical model assuming that the effects result from choosing the wrong task (Meiran & Daichman, 2005). The patients in this study also exhibited especially increased error rates in incongruent switch trials. Second, congruency effects are increased in conditions where task switching does not involve (or involves less) suppression of the abandoned task set (Arbuthnott, 2005). Third, participants who anticipate a task switch (but do not execute such a switch) show RT congruency effects, whereas participants who do not expect a switch (and also do not switch) do not show these effects (Yehene, Meiran, & Soroker, 2005), suggesting that the source of conflict originates with configuring the appropriate task set rather than determining a particular response. Finally, using a computational model of task switching, Brown et al. (2006) explicitly suggest that the conflict in incongruent trials is resolved by enhancing task-related representations.

Nevertheless, there is some suggestion from the present study that points to conflict between S–R rules as the source of interference. We carried out a secondary analysis of RTs and errors, examining the effect of repeating or changing the stimulus from the preceding trial and requiring either a response repetition or a new response. Typically, such analyses show that controls experience more difficulty in repeating a response to a changed stimulus than to a repeated stimulus, and have more difficulty changing to a different response if the stimulus repeats than if it switches (e.g., Hommel & Colzato, 2004). No interesting differences emerged between patients and controls in RTs, but the pattern of errors was informative. Specifically, irrespective of whether the task switched or repeated, patients made more errors when the stimulus changed but required a repeated response, as compared to controls, but only when there was response conflict. Given that appropriate task sets can be configured in advance of stimulus onset, the finding that stimulus repetition strongly influences patients' performance points to conflict at the level of S–R representations, rather than task set–response representations. The absence of reliable effects of manipulating the time available for advance configuration of task and response sets (CTI) on congruency effects is also consistent with this view. Given that we did not manipulate variables that allow for directly testing among these alternatives, we leave the question of the source of interference in this task context for future research.

## How is the Cerebellum Involved in Conflict Resolution?

The cerebellum contains over half of all of the neurons in the brain (Zagon, McLaughlin, & Smith, 1977) and has undergone significant alteration through hominid evolution. The functional role of any region of the cerebellum is likelier to be determined by its connections rather than by any intrinsic, local cerebellar specialization. These connections have been systematically mapped using the trans-synaptic vector Herpes Simplex Virus type 1, and they have been found to preferentially distribute to the PFC (Middleton & Strick, 2001). Lesion studies consistently demonstrate cognitive impairments following cerebellar damage that resemble those seen in patients with PFC lesions (e.g., disturbances in various domains of attention, and reduced capacity for strategic and generative tasks). Functional imaging studies in healthy subjects consistently demonstrate parallel activations in the PFC and cerebellar regions on similar tasks even when there are no motor demands. The detailed knowledge of cerebellar anatomy and critical projections to and from the PFC provide a structural explanation for the close functional relationship between these structures in normal function and in disease.

The present finding that patients had difficulty with suppressing the irrelevant task-set on incongruent trials suggests an important role for the cerebellum in conflict resolution. However, given the neuroanatomical evidence reviewed above, it is unlikely that the cerebellum would accomplish this task in isolation. Thus, it is worth considering how the cerebellum might work in concert with other cortical areas in conflict resolution.

One area with which the cerebellum shares extensive connectivity is the PFC. Support for the important

neural interactions between the cerebellum and the PFC comes from brain imaging studies of task-set switching (Konishi, Chikazoe, Jimura, Asari, & Miyashita, 2005; Konishi, Jimura, Asari, & Miyashita, 2003). These studies used a modified Wisconsin Card Sorting Test (WCST) that required subjects to reconfigure a new task set that was either congruent or incongruent with the previously adopted task set. Depending on the task demands, these studies have typically implicated areas of the superior (Konishi et al., 2003) and anterior PFC (Konishi et al., 2005). Interestingly, in addition to prefrontal activation, Konishi et al. (2005) report activation in the cerebellum during situations requiring the inhibition of a previous task set (analogous to the incongruent condition in the present study); however, they do not address this finding. This finding is in line with the results of the present study and offers further support for a critical role for the cerebellum in overcoming the influence of set interference, particularly in situations of response conflict.

In addition to task-set switching, a number of behavioral studies using the present paradigm provide results that also implicate the PFC in conflict resolution. Meiran et al. (2001) investigated response conflict in aging, believed to disproportionately impair PFC functioning, and Meiran, Friedman, and Yehene (2004) studied response conflict in Parkinson's disease, a condition affecting frontal–subcortical circuits. In both of these studies, the target population exhibited greater congruency effects as compared to their respective controls, suggesting impaired conflict resolution. These studies, in conjunction with the present findings, suggest that conflict resolution could be mediated by a frontal–cerebellar circuit.

## Implications for Extant Models of Cerebellar Cognitive Processing

The present findings are informative with respect to the role of the cortico-cerebellar system in cognitive processing, which has been a puzzle for many decades. Ramnani (2006) recently proposed an account of how frontal and cerebellar circuits interact to guide information processing. This account borrows from the internal model hypothesis by Ito (1993, 2005), and suggests, in comparison with the necessarily flexible and readily adaptive circuitry of the frontal lobes, cerebellar circuits are relatively inflexible and static. It is argued that information processing carried out by the cerebellum mimics that undertaken in cortical structures, but can be carried out more rapidly by an established cerebellar circuit than by its cortical counterpart. This advantage in speed, however, comes at the expense of flexibility. Specifically, cerebellar learning should be context-specific and difficult to modify as contextual demands change. Such demands are argued to be better suited to the PFC, which can flexibly modify behavior in order to comply with modified task demands. The cerebellum in this account thus serves to reduce processing demands on the PFC, freeing it up for tackling more complex cognitive operations.

Our results are in line with this proposal and provide evidence that the cerebellum is not essential for processing all tasks associated with the PFC. In the absence of response conflict, task-switching abilities were intact in our patients contrary to previous results in neuroimaging (Dreher et al., 2002; Le et al., 1998) and studies in children with cerebellar lesions (Berger et al., 2005). Given that task switching requires flexible modification of reassigning responses to task sets and that the cerebellum is argued to be suboptimal for such processing (Ramnani, 2006), it is, perhaps, not surprising that our patients were unimpaired in this respect (see also Bischoff-Grethe, Ivry, & Grafton, 2002). However, the fact that our patients were impaired during conflict resolution, ostensibly another frontal task, suggests that the cerebellum makes a specific contribution to this aspect of cognitive functioning. In line with Ramnani (2006) and Ito (1993, 2005), we suggest that the intact cerebellum may be critical for PFC circuitry to efficiently process the more routine aspects of a task. Any damage to cerebellar circuitry would result in additional processing demands, further depleting available PFC (and other cortical) resources, producing impairments similar to those observed in elderly populations (Meiran et al., 2001). Further research is needed to address this hypothesis by examining a wide array of cognitive tasks to provide converging evidence for the specific role of the cerebellum in cognitive processing.

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