Research Report

Short- and long-term changes in anterior cingulate activation during resolution of task-set competition

Todd S. Woodward[a,b,*], Christian C. Ruff[c], Elton T.C. Ngan[d]

[a]Department of Research, Riverview Hospital, Coquitlam, Canada
[b]Department of Psychology, Simon Fraser University, Burnaby, Canada
[c]Institute of Cognitive Neuroscience, University College, London, UK
[d]Department of Psychiatry, University of British Columbia, Vancouver, Canada

A R T I C L E   I N F O

A B S T R A C T

Alternating between task sets involves detection that the current task set is unfavorable, initiation of a change in set, and application of the new task set while fine-tuning to optimally adjust to the demands of the environment. Functional magnetic resonance imaging (fMRI) studies of cognitive flexibility consistently report activation of the anterior cingulate cortex and/or adjacent pre-supplementary motor regions (ACC/pre-SMA, medial Brodmann's areas 24/32/6), suggesting that these cortical regions are involved in switching task set. In the current study, our objective was to probe whether ACC/pre-SMA activation would decrease for a number of trials following a switch in task set, implying longer-term involvement in fine-tuning adjustments. By measuring activation when switching between word reading and color naming in response to Stroop stimuli, ACC/pre-SMA activation was observed when actively countering the influence of the irrelevant task set, and this activation decreased as a function of the number of trials since a task switch. Basal ganglia and thalamic regions also displayed a decreased response over successive trials after task switches. These findings suggest that the ACC/pre-SMA are not only involved in generating a new course of action, but are also involved (along with subcortical regions) in fine-tuning operations that resolve competition between task sets over subsequent repetitions of the same task.

1.   Introduction

Cognitive flexibility largely defines human behavior. Success in this regard rests on the ability to detect that the current trajectory is unfavorable, to initiate a change by stopping the current cognitive set, and to implement a new one and fine-tune the system to optimally adjust to the novel demands of the environment. Studies of these components of cognitive flexibility have produced a wealth of knowledge in cognitive psychology and neuropsychology. Examples include studies on task switching (Allport et al., 1994; Monsell, 1996; Woodward et al., 2002, 2003), attention shifting (Wager et al., 2004), set shifting (Owen et al., 1991), error processing (Holroyd and Coles, 2002), conflict monitoring (Botvinick et al., 2001), and response inhibition (Booth et al., 2003). Studies of cognitive flexibility involve switching between and managing *task sets*, defined as the package of stimulus–response mappings and instructional requirements associated with a given task trajectory (Monsell et al., 2000).

* Corresponding author. Room 105, Department of Research, Administration Building, Riverview Hospital, 2601 Lougheed Highway, Coquitlam, B.C., Canada V3C 4J2. Fax: +1 604 524 7145.
  E-mail address: toddswoodward@gmail.com (T.S. Woodward).

Table 1 – Response time (RT), standard deviations (in brackets), and errors for manual response time in all experimental conditions

	Response time	% Correct
Color naming		
Color neutral	792 ms (198 ms)	99
Color incongruent	1007 ms (233 ms)	94
Stroop effect	215 ms***	
Word-reading segment A		
Word neutral	714 ms (207 ms)	99
Word incongruent	897 ms (258 ms)	94
Reverse-Stroop early	184 ms***	
Word-reading segment B		
Word neutral	674 ms (170 ms)	99
Word incongruent	733 ms (163 ms)	96
Reverse-Stroop late	59 ms***	

*** $P < 0.001$.

Functional magnetic resonance imaging (fMRI) studies of these cognitive paradigms consistently report activation of the anterior cingulate cortex and/or adjacent pre-supplementary motor regions (ACC/pre-SMA, medial Brodmann's areas 24/32/6; Ruff et al., 2001; van Veen et al., 2001; Barch et al., 2000; Luks et al., 2002; Milham et al., 2001; Gehring and Knight, 2000; Holroyd et al., 2004; Rushworth et al., 2002; Duncan and Owen, 2000; Liu et al., 2004; Kondo et al., 2004), and these regions are consistently identified in pertinent review papers (Wager et al., 2004; Cabeza and Nyberg, 2000; Botvinick et al., 2004). As may be expected from the observation that ACC/pre-SMA activation is elicited during a wide range of information processing requirements, the precise role of the ACC/pre-SMA has been intensely debated. Some early theorists suggested that the ACC/pre-SMA implements top–down processes that modulate conflict between neuronal processing streams (Posner and Rothbart, 1998; Petersen et al., 1988, 1999; Pardo et al., 1990), while others suggested that the ACC/pre-SMA serves as a generic "conflict detector", signaling the need for top–down cognitive control to other regions (Botvinick et al., 1999; Carter et al., 2000; MacDonald et al., 2000; Cohen et al., 2000). What is currently emerging as a common theme to these divergent interpretations of ACC/pre-SMA function is that this cortical region is involved in implementing a new course of action through error-alerting (BAs 24/32) and response modification/selection (rostral BA 6; Volz et al., 2003; Gehring and Taylor, 2004; Ridderinkhof et al., 2004; Rushworth et al., 2004).

Task switching studies have been at the forefront of the challenge to clarify the function of the ACC/pre-SMA. In some task switching paradigms, one trial is enough for complete recovery (Monsell et al., 2003); however, in others, competition between task sets can be detected for many trials after a switch has taken place (Wylie and Allport, 2000; Allport and Wylie, 1999, 2000). In a recent fMRI study (Wylie et al., 2004), it was confirmed that, under some conditions, the neural activations associated with a switched-from task can persist over many trials after the switch. Such paradigms provide the opportunity to test whether activation in the ACC/pre-SMA is simply all-or-none or if it functions in a graded fashion, decaying as a function of the number of trials since a switch as the new course of action becomes routine. Our objective was to assess

the involvement of the ACC/pre-SMA in the fine-tuning operations that resolve competition between task sets with subsequent repetitions of the same task.

Stroop stimuli are color words created such that the semantic meaning of the word is incongruent with respect to the color in which the word is written (e.g., the word "RED" printed in blue ink). Under normal conditions, color naming is slowed for incongruent as compared to neutral stimuli (e.g., naming the color of XXXX), and this is referred to as Stroop interference. The converse type of interference, slowing of word reading due to an incongruent print color, is referred to as reverse-Stroop interference. Reverse-Stroop interference does not occur under most circumstances but is a robust phenomenon when switching between word reading and color naming on a trial-by-trial basis. This is thought to be attributable to reactivating the previously suppressed word-reading task set when processing incongruent (but not neutral) Stroop stimuli (Allport et al., 1994). The important point for the current study is that reverse-Stroop interference is elicited when switching only infrequently between color naming and word reading, and in contrast to other task switching effects which resolve after one trial (Monsell et al., 2003), reverse-Stroop interference dissipates rather slowly as incongruent word reading is repeated in the absence of incongruent color naming (Wylie and Allport, 2000; Allport and Wylie, 1999, 2000). In a previous study, we observed strong activation in the ACC/pre-SMA for reverse-Stroop interference when encountering persisting set from the color-naming trial immediately prior to word reading (Ruff et al., 2001), but whether and how this activation would decay with repeated word-reading trials has not yet been tested.

Here, we attempted to characterize activation changes in ACC/pre-SMA that follow the decay in reverse-Stroop interference on a trial-by-trial basis. We modeled decreasing activity over successive instances of incongruent word reading in order to test for a linear ACC/pre-SMA trajectory of activation over successive incongruent word-reading trials. We expected that ACC/pre-SMA activation would decay with the number of trials since a task switch, reflecting involvement in fine-tuning after a task switch.

2. Results

2.1. Behavioral

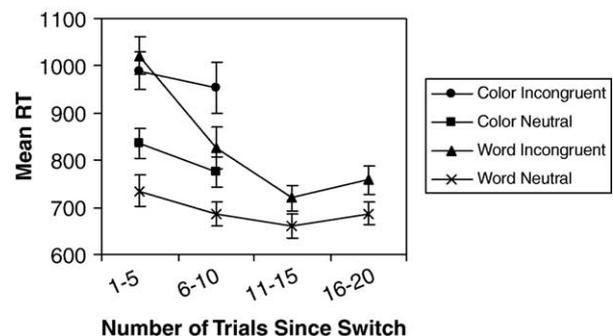Means and standard deviations of manual response times in all experimental conditions are displayed in Table 1. The

Fig. 1 – Means and standard errors for response time (RT) for each response type plotted as a function of number of trials since a task switch.

Table 2 – Talairach coordinates and results of event-related analysis for Stroop effect (contrast of incongruent color naming and neutral color naming conditions)

Cluster size	Peak locations	Peak BAs	Peak T (Z)	x	y	z
94	Cingulate gyrus	32	9.03 (4.75)	−4	14	40
	Cingulate gyrus	32	6.11 (3.96)	4	25	32
22	Middle frontal gyrus	46	6.65 (4.13)	−44	21	25
	Middle frontal gyrus	46	5.32 (3.67)	−48	28	24

Inference was performed using a random effects analysis at the voxel level at $P < 0.001$ and the cluster level at $P < 0.05$ corrected.

Stroop and reverse-Stroop effects were computed by subtracting mean response times in the incongruent condition from those in the neutral condition for color naming and word reading, respectively. Significant behavioral interference was observed for the Stroop effect (215 ms), $t(11) = 6.56$, $P < 0.001$), reverse-Stroop effect segment A (RS-Early; 184 ms), $t(11) = 8.67$, $P < 0.001$, and reverse-Stroop effect segment B (RS-Late; 59 ms), $t(11) = 6.39$, $P < 0.001$. One-tailed t tests revealed that RS-Late differed significantly from both the Stroop effect, $t(11) = 4.33$, $P < 0.001$, and from RS-Early, $t(11) = 5.11$, $P < 0.001$, but RS-Early did not differ significantly from the Stroop effect, $t(11) = 0.94$, $P = 0.18$. Accuracy was high in all conditions, never falling below 94%, and was not analyzed further.

Word-reading RTs were submitted to a 4 × 2 repeated-measures ANOVA, incorporating number of trials since a switch from color naming (1–5, 6–10, 11–15, and 16–20) as factor 1 and incongruency (neutral vs. incongruent) as factor 2. The mean RTs are presented in Fig. 1. This analysis resulted in significant main effects of trials since a switch, $F(3,33) = 37.21$, $P < 0.001$, and incongruency, $F(1,11) = 144.08$, $P < 0.001$, and a significant interaction, $F(3,33) = 14.94$, $P < 0.001$. ANOVAs carried out separately for incongruent and neutral stimuli demonstrated that the effect of trials since a switch was highly significant for the incongruent word-reading trials, $F(3,33) = 34.65$, $P < 0.001$, but only marginally significant for the neutral word-reading trials, $F(3,33) = 3.98$, $P = 0.05$. This analysis demonstrated that, as predicted, the reverse-Stroop effect (incongruent-neutral word reading) faded with number of trials since a switch from color naming.

2.2. Imaging

To analyze the ACC/pre-SMA activations associated with actively countering the irrelevant task set, we specified contrasts for the comparison of incongruent versus neutral stimuli of interest using the random effects method implemented in SPM99 (Stroop, RS-Early and RS-Late). As can be seen from the behavioral results (Fig. 1), RS-Early effects appeared to remain substantial for up to 10 trials and were thus analyzed independently to assess actively countering the irrelevant task set. In contrast, RS-Late trials were expected to show no ACC/pre-SMA activation because the task change appeared largely complete after trial 10.

During Stroop interference (see Table 2), one large cluster was located in the ACC/pre-SMA (see Fig. 2), with two peaks in BA 32, extending into rostral BA 6. For RS-Early, we observed more widespread activation with 8 clusters (see Table 3). One of these clusters was located in the ACC/pre-SMA (as was the case for the Stroop effect, see Fig. 3), with two peaks in BA 32, extending into rostral BA 6. As predicted, no activation was detected for the contrast of incongruent versus neutral RS-late trials.

The results of the parametric modulation analysis (designed to assess decay of activation over repeated word-reading trials; see Table 4) demonstrated that activity of the ACC/pre-SMA during incongruent but not neutral word-reading trials displayed a linear decay in activity as a function of distance from color naming. The regions that maximally displayed this pattern of linear decay were located in BA 32, extending into rostral BA 6 (see Fig. 4). Other areas that followed this trajectory during incongruent word-reading trials were located in sensorimotor and parietal cortex, as well as in cerebellum, thalamus, and basal ganglia. Fig. 5 shows the hemodynamic response to incongruent and neutral word-reading trials in the ACC/pre-SMA activation peak, averaged over subjects, and plotted as a function of lag from color-naming trials. This shows that the ACC/pre-SMA peak response reduced linearly with the maximum distance from the task switch for incongruent word-reading trials, whereas no changes in the ACC/pre-SMA were
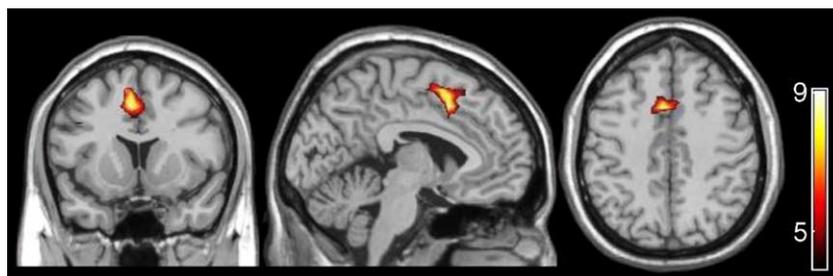

Fig. 2 – Activation for the Stroop effect (contrast of incongruent color naming and neutral color naming conditions) rendered as Z scores on the MNI template brain according to the color scale given to the right of the panel. Inference was performed using a random effects analysis at the voxel level at $P < 0.001$ and the cluster level at $P < 0.05$ corrected. Images are displayed in neurological convention (left is left). Slices are displayed at ACC/pre-SMA cluster peak, Talairach coordinates $x = −4$, $y = 14$, $z = 40$.

Table 3 – Talairach coordinates and results of event-related analysis for reverse-Stroop segment A effect (i.e., RS-Early, incongruent word reading–neutral word reading, first 10 trials immediately following a switch from color naming)

Cluster size	Peak locations	Peak BAs	Peak T (Z)	x	y	z
54	Medial frontal gyrus	32	8.06 (4.52)	–8	10	44
	Cingulate gyrus	32	5.64 (3.79)	4	21	39
61	Precentral gyrus	6	8.26 (4.57)	–36	5	22
	Inferior frontal gyrus	9	7.43 (4.36)	–44	5	26
	Inferior frontal gyrus	45	4.74 (3.43)	–48	20	17
28	Middle frontal gyrus	6	6.70 (4.15)	32	3	51
	Middle frontal gyrus	6	5.60 (3.78)	44	6	51
18	Postcentral gyrus	2	6.43 (4.06)	36	–25	38
21	Inferior parietal lobule	40	5.72 (3.82)	–40	–48	43
	Inferior parietal lobule	40	4.81 (3.46)	–44	–37	39
	Inferior parietal lobule	40	4.29 (3.22)	–51	–37	42
44	Putamen inferior	*	12.78 (5.42)	–24	11	–4
	Frontal gyrus	47	6.58 (4.11)	–36	15	–7
	Caudate body	*	4.93 (3.51)	–12	12	7
38	Pulvinar	*	7.24 (4.30)	–20	–23	5
	Thalamus	*	6.31 (4.02)	–12	–8	4
15	Thalamus	*	6.90 (4.21)	0	–19	1
	Midbrain	*	4.84 (3.47)	–8	–23	–2

Inference was performed using a random effects analysis at the voxel level at P < 0.005 and the cluster level at P < 0.05 corrected.

Table 4 – Talairach coordinates and results of event-related analysis for parametric modulation of incongruent word reading

Cluster size	Peak location	Peak BAs	Peak T (Z)	x	y	z
20	Cingulate gyrus	32	4.36 (3.25)	–4	18	40
128	Superior frontal gyrus	6	8.69 (4.67)	20	–8	63
	Postcentral gyrus	3	6.68 (4.14)	36	–25	45
	Postcentral gyrus	3	4.54 (3.34)	44	–20	56
15	Precuneus	7	3.69 (2.91)	–4	–72	44
	Precuneus	19	3.37 (2.74)	–8	–80	37
	Precuneus	7	3.25 (2.67)	0	–76	37
25	Medial globus pallidus	*	6.02 (3.92)	–12	0	0
	Caudate head	*	5.92 (3.89)	–8	12	3
40	Thalamus	*	5.29 (3.66)	20	–15	12
	Thalamus	*	3.98 (3.07)	4	–7	8
	Caudate body	*	3.60 (2.87)	12	8	7
41	Culmen (Cerebellum)	*	8.01 (4.51)	–24	–52	–21
	Culmen (Cerebellum)	*	3.19 (2.63)	–8	–55	–11

Inference was performed using a random effects analysis at the voxel level at P < 0.005.

detectable for neutral trials. For neutral trials, the only cluster that reduced significantly with trials since a task switch was a small cluster (26 voxels) in the cerebellum/lingual gyrus, with a peak at x = 0, y = –90, z = –9, t = 5.92.

3. Discussion

Switching task sets involves detection that the current task set is unfavorable, initiation of a change in task set by stopping the current task set and implementing a new one, and application of the new task set while fine-tuning to optimally adjust to the demands of the environment. Functional magnetic resonance imaging (fMRI) studies of cognitive flexibility consistently report activation of the ACC/pre-SMA and posit that that this cortical region is critically involved in monitoring/implementing adaptive adjustments to the current task set (Gehring and Taylor, 2004; Ridderinkhof et al.,

2004; Rushworth et al., 2004; Ullsperger and von Cramon, 2004). In the current study, our objective was to probe for decreases in the activation of the ACC/pre-SMA as a function of the number of trials from a task switch, reflecting fine-tuning processes. As predicted, ACC/pre-SMA activation was observed not only when actively countering the influence of the irrelevant task set (the RS-Early condition), but also displayed a linear decrease in activation with number of trials since a switch from color naming. Also following this trajectory were sensorimotor, parietal, cerebellar, thalamic, and basal ganglia regions.

Some aspects of ACC/pre-SMA activation are presumably common to Stroop and reverse-Stroop interference. Namely, the common dorsal ACC (BA 24/32) may serve as a detector of conflict, a detector of error, or a detector of the need to change the course of action due to an unwanted set of circumstances, and the common pre-SMA activation may reflect the response set selection required to overcome this interference (Volz et al., 2003; Gehring and Taylor, 2004). Reverse-Stroop interference is attributable to competition between the color-naming and word-reading task rules (Wylie and Allport, 2000; Allport and Wylie, 1999, 2000; Allport et al., 1994; Monsell et al., 2001; Yeung and Monsell, 2003), and this competition dissipates slowly with repeated word reading as the currently relevant

Fig. 3 – Activation for reverse-Stroop effect segment A (incongruent word reading–neutral word reading, immediately following a switch from color naming) displayed with the same conventions as for Fig. 2. Slices are displayed at ACC/pre-SMA cluster peak, Talairach coordinates x = –8, y = 10, z = 44.
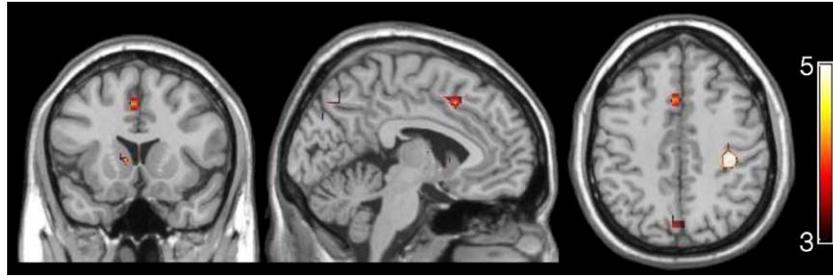
Fig. 4 – Activation for parametric modulation of incongruent word reading (assessing decay of activation over repeated word-reading trials), rendered as Z scores on the MNI template brain according to the color scale given to the right of the panel. Inference was performed using a random effects analysis at the voxel level at *P* < 0.005. Images are displayed in neurological convention (left is left). Slices are displayed at ACC/pre-SMA cluster peak, Talairach coordinates *x* = −4, *y* = 18, *z* = 40.

task set biases the settling of the system to an efficient state (Wylie et al., 2004). Thus, for reverse-Stroop interference, as the number of trials since a task switch increases, task-set competition decreases, ACC activation decreases, and pre-SMA activation decreases due to a reduced demand for response set selection.

In addition to the similarities between activation patterns induced by Stroop and reverse-Stroop interference, important differences were also observed. Namely, while Stroop activation was exclusively cortical, reverse-Stroop interference involved activation of subcortical regions as well, for which activation linearly decreased with trials since a switch from color naming. This is in accordance with anatomical connections as the basal ganglia interacts with the ACC/pre-SMA via the thalamus (Alexander and Crutcher, 1990; Alexander et al., 1986; Penny and Young, 1983), a connection thought to mediate adjustment of competing stimulus–response mappings (Taylor and Saint-Cyr, 1992; Mink, 1996; Frank, 2005). Such adjustments are required for the fine-

tuning involved in repeated word reading in the presence of competing task sets; thus, the adjustments required for *reversal* of an information processing bias away from the dominant task set may require subcortical neural systems (in concert with the ACC/pre-SMA; Ruff et al., 2001) to a greater extent than does *instantiation* of that bias.

Within the task switching literature, substantial discussion has been devoted to the topic of whether reductions in task-set competition (as was observed in the current experiment) are attributable to a top–down control system implementing fine-tuning over an extended period of time, to passive decay of task-set competition, or to both (Logan, 2003; Wylie and Allport, 2000; Monsell et al., 2003; Yeung and Monsell, 2003). The contribution that the current data can make to this debate is not conclusive, but a clue can be derived from the distinct patterns of activation associated with Stroop versus reverse-Stroop interference. Namely, countering reverse-Stroop interference appears to elicit more subcortical involvement than countering Stroop
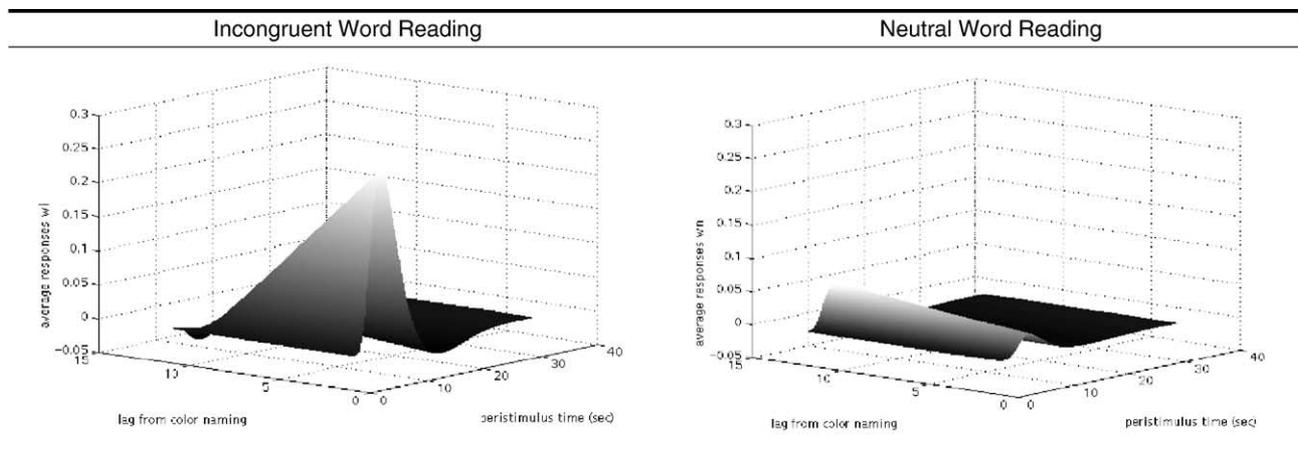

Fig. 5 – Plots of the estimated modulation (i.e., fitted responses in percent global brain signal) of event-related activity in response to incongruent and neutral word-reading trials for the peak ACC/pre-SMA voxel (*x* = −4, *y* = 18, *z* = 40, BA 32). The figure demonstrates that the ACC/pre-SMA hemodynamic responses to incongruent word-reading trials decrease in parallel with the lag from the task switch, whereas no change is estimated for neutral word reading. This style of plot is provided by SPM99 for individual subjects, but the current figure is averaged over all subjects. *Peristimulus time* (seconds) refers to the number of seconds from the time that the stimulus of interest was presented, and the estimated hemodynamic response is plotted along this dimension (Friston et al., 1998, pp. 34–35). The third dimension for this plot is labeled *lag from color naming* and refers to the number of word-reading trials since a switch from color naming.

interference. Considering the involvement of the basal ganglia in adjustment of stimulus–response mappings (Taylor and Saint-Cyr, 1992; Mink, 1996; Frank, 2005), it is tempting to conclude that top–down control is applied on each trial, leading to trial-by-trial reductions in TSI. However, the current set of results cannot conclusively determine whether the trial-by-trial reduction in TSI can be attributed to such a top–down cortical–subcortical control system implementing response set selection (involving the basal ganglia and pre-SMA).

Both our present and previous findings (Ruff et al., 2001, Fig. 1) suggest that (1) the ACC/pre-SMA activation observed for both Stroop and reverse-Stroop interference reflects the role of implementing a new course of action through error-alerting (BAs 24/32) and response modification/selection (rostral BA 6; Volz et al., 2003; Gehring and Taylor, 2004) and (2) the subcortical regions (thalamus and basal ganglia) active exclusively during the processing of reverse-Stroop interference are linked to the reversal of a bias against the dominant task set. Theoretical accounts of cognitive flexibility typically focus on short-term changes, such as detecting that a change is needed, stopping the current behavior, or implementing a new one. The current study emphasizes that fine-tuning the system to optimally adjust to the demands of the environment (e.g., the reversal of a response-set bias) can take place over an extended period of time and that the neural system encoding this aspect partially overlaps with the structures involved in the short-term implementation of a new task set.

4. Experimental procedures

4.1. Participants

Twelve right handed, healthy, native English speakers (4 women, mean age = 34.5 years, SD = 10.03) were recruited by advertisement from the community of Vancouver, British Columbia, and outlying regions. All subjects had 20/20 or corrected to 20/20 vision and normal color vision. Participants underwent screening for MRI compatibility, and informed consent was obtained from subjects after the nature of the experimental procedures was explained. The procedures administered complied with University ethical approval.

4.2. Materials

All stimuli were displayed in 38-point Helvetica font, centered on the screen, and displayed against a gray background, subtending a visual angle of 2 × 6°. For the incongruent color-naming and word-reading stimuli, we used the color words RED, GREEN, BLUE, and YELLOW displayed in incongruent print colors red, green, blue, or yellow. Presented stimuli were randomly selected (with replacement) from all incongruent word/print combinations and presented in the same order for all subjects. For the color-naming neutral stimuli, we presented a string of four Xs displayed in red, green, blue, or yellow print. For the word-reading neutral stimuli, we used the words RED, GREEN, BLUE, and YELLOW displayed in black print. Two instruction screens were also prepared for the scanning session, consisting of the phrases "WORD" and "COLOR", displayed in black print. The instruction screens were used to cue a task switch. Finally, a "+" character in black print was used as a fixation point.

4.3. Procedure

4.3.1. Training

For the training session, subjects were informed that they would be required to read color words presented on the screen and were instructed to respond manually with the following finger–color correspondences: left index finger RED, left middle finger GREEN, right index finger YELLOW, and right middle finger BLUE. Stimuli were randomly selected from the incongruent and neutral word-reading stimuli, and 50% were printed in black "ink", while the other 50% were printed in one of the incongruent print colors. Each stimulus remained on the screen until the subjects responded, and the ISI between stimuli was 100 ms. Feedback for errors ("Incorrect") or slow responses exceeding 1300 ms ("Too slow") appeared on the screen for 2 s before the next color word was presented. Each subject completed 15 min of training, and all subjects had extinguished incorrect and slow responses on completion.

4.3.2. Scanning

Scanning trials were performed in a darkened room, with stimuli presented on a rear projection screen mounted at the entrance to the magnet bore. Participants viewed the screen by means of a mirror system attached to the head coil. Stimuli were presented using in-house software (Visual Auditory Presentation Package; http://nilab. psychiatry.ubc.ca/vapp/). Two commercially available MRI compatible fiber optic response devices with two buttons each were used for the subjects' responses. For trials that required a response, the fixation point was presented for 900 ms, immediately followed by the imperative stimulus for 1900 ms, and then by a blank screen for 100 ms. The response was always recorded within the 1900 ms that the stimulus remained on the screen, which did not affect stimulus presentation time. Using this methodology, the stimulus onset asynchrony was 2900 ms, allowing the presentation of events to be jittered in steps of 0.1 s over the TR time of 3 s. The random presentation of the incongruent and neutral Stroop stimuli also contributed to the distribution of events of interest over the TR time of 3 s. For all scanning runs, instruction screens ("WORD" or "COLOR") were displayed for 8900 ms followed by a blank screen for 100 ms. Instruction screens were presented when a task switch was required.

Before each scanning run, standardized instructions were read to the subject. For example, subjects were instructed: "You will now be required to either press for words, or press for the color of the ink in which the words are written. Instructions on the screen will tell you whether to press for word or press for color. Please respond as quickly and as accurately as possible." The practice run consisted of 10 word-reading trials (5 neutral and 5 incongruent in random order) followed by 10 color-naming trials (5 neutral and 5 incongruent in random order) and 60 word-reading trials (30 neutral and 30 incongruent in random order). The purpose of this practice run was to introduce the color-naming task in the first 20 trials and to give ample opportunity for the subjects to re-familiarize themselves with the finger-color correspondences while in the scanner on the last 60 trials and to bring to baseline the interference generated on the practice incongruent color-naming trials.

The experimental run involved switching between word reading and color naming and lasted 672 s. A total of 186 trials were presented. The first six trials were word-reading trials (three neutral and three incongruent) and were considered practice. The seventh trial was a color-naming trial, and this constituted the first task switch. Over the remaining 179 trials, the task was switched 11 more times. Ten color-naming trials always alternated with twenty word-reading trials. Each time the task was to be switched, an instruction screen was displayed. On any given trial, either a task-appropriate neutral or incongruent stimulus was selected with a probability of 0.50. In total, 30 incongruent and 30 neutral color-naming trials and 60 incongruent and 60 neutral word-reading trials were presented. Twice as many word-reading trials were presented because the

reverse-Stroop effect is thought to reduce with distance from incongruent color-naming trials (Allport and Wylie, 2000). Since we expected the reverse-Stroop effect to be greatly diminished after 10 word-reading trials, the last 10 word-reading trials of each series would serve to bring the reverse-Stroop effect back to baseline levels. We refer to the first 10 word-reading trials following a switch from color naming as *word*-reading *segment A* and the last 10 word-reading trials following a switch from color naming as *word*-reading *segment B*. "Early" reverse-Stroop (RS-Early) and "late" reverse-Stroop (RS-Late) effects were computed as neutral subtracted from incongruent stimulus conditions for word-reading segment A and word-reading segment B, respectively. Example trials are presented in Fig. 6.

4.4. Processing and analysis

4.4.1. Image processing

Images were acquired with a clinical GE 1.5 T whole body MRI system fitted with a Horizon echo speed upgrade. The participant's head was firmly secured using a custom head holder. Blood oxygen level dependent (BOLD) contrast images were collected with a gradient-echo sequence (TR/TE 3000/40 ms, flip angle 90°, FOV 24 × 24 cm, 64 × 64 matrix, 62.5 kHz bandwidth, 3.75 × 3.75 mm in plane resolution, 5 mm slice thickness, 29 slices), effectively covering the whole brain (145 mm axial extent, no spacing between 5 mm slices). In the experimental run, a total of 224 images of the entire brain were collected in a period of 672 s. The run was preceded by a 12 s rest condition, allowing T1 effects to stabilize. The four brain volumes collected during this period were not included in any subsequent analyses.

Functional images were reconstructed offline and independently realigned and motion corrected using the method implemented in SPM99 (Statistical Parametrical Mapping 99, 1999). Translation and rotation corrections did not exceed 3 mm or 3° for any of the participants. Parameters for spatial normalization were determined using mean functional images constructed from the realigned images of each session (i.e., participant). All coordinates given in this article refer to original Talairach space. The normalized functional images were smoothed with an 8 mm full width at half maximum Gaussian filter. Low frequency noise was removed using a 0.1 Hz high pass filter.

4.4.2. Data analysis

4.4.2.1. *Actively countering an irrelevant task set.* The event-related responses to all events were modeled using a series of appropriately placed delta functions convolved with the synthetic hemodynamic response function implemented in SPM99. This hemodynamic response function comprises the sum of two gamma functions and has been found to provide a reasonable and comprehensive model of the hemodynamic response (Friston et al., 1994, 1998; Boynton et al., 1996). For each of the scan series, the model of the composite hemodynamic response for the entire run comprised a sequence of appropriately placed synthetic responses to six different events: (1) 30 neutral and (2) 30 incongruent color-naming trials, (3) 30 neutral and (4) 30 incongruent word-reading trials immediately following color-naming trials (word reading segment A), (5) 30 neutral and (6) 30 incongruent word-reading trials following these word-reading trials (word reading segment B). The general linear model
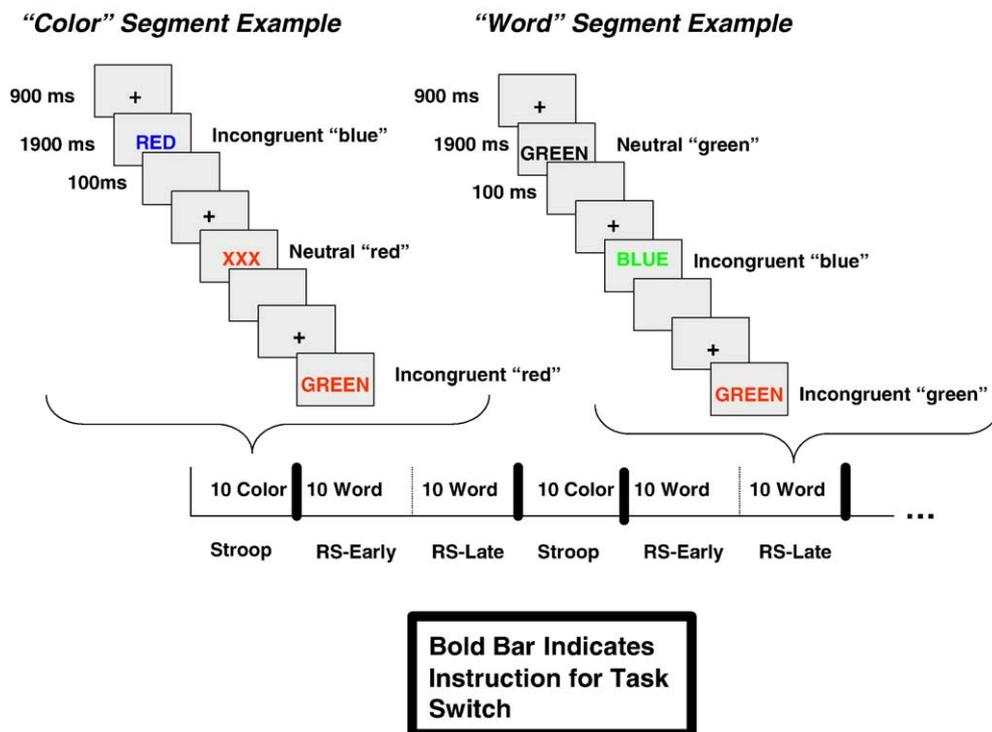

Fig. 6 – Visual depiction of the experimental run. The insets provide examples of color naming and word-reading trials. In total, 60 color naming and 120 word-reading trials were presented. The instructions for a task switch consisted of "WORD" and "COLOR". We refer to the first 10 word-reading trials following a switch from color naming as *word*-reading *segment A* and the last 10 word-reading trials following a switch from color naming as *word*-reading *segment B*. "Early" reverse-Stroop (RS-Early) and "late" reverse-Stroop (RS-Late) are computed as the subtraction incongruent minus neutral stimulus conditions for word-reading segment A and word-reading segment B, respectively. Please see the Experimental procedures section for a more detailed explanation of the experimental task run.

approach implemented in SPM99 thus allowed us to estimate, and statistically compare, parameters for the influence of each of these event conditions on the hemodynamic response in each voxel under consideration. By specifying and calculating contrasts between incongruent and neutral event conditions, we thus obtained estimates of (and statistical values for) the increase of activation in each voxel in response to incongruent as compared to neutral stimuli (i.e., the Stroop effect, reverse-Stroop effect for segment A [RS-Early], and reverse-Stroop effect for segment B [RS-Late]). Inference was performed using a random effects analysis, thresholded at the voxel level at $P < 0.001$ ($t = 4.02$) for basic analyses and the cluster level at $P < 0.05$ corrected ($k = 15$). ACC/pre-SMA activation was expected for RS-Early trials, which are presumably heavily influenced by the implementation of a task change, but not for RS-Late trials, for which the task change should be largely complete.

4.4.2.2. *Decay of activation over optimization trials.* We directly investigated the modulation of activation during both incongruent and neutral word reading within a second model, using the parametric modulation approach as implemented in SPM99. In these models, the word-reading trials were not separated into segment A and B; instead, modulation of activation was assessed over all 20 word-reading trials following a switch from color naming. The models contained four covariates representing neutral and incongruent color naming or word-reading trials, respectively, and two additional covariates for linear modulation of the hemodynamic response to each word-reading trial, as a function of the number of word-reading trials since the switch from color naming. An exponential model was also fitted for exploratory purposes but is not reported in detail as it produced null results. The condition-specific vector values specifying the parametric modulation were assigned as follows: the trial immediately following a switch from color naming (n) was assigned the integer 1, trial $n + 1$ was assigned the integer 2, trials $n + 2$ was assigned the integer 3, continuing up to the word-reading trial preceding the subsequent task switch back to color naming or the end of the experiment (in the case of the terminal segment of word-reading trials). Number of trials since a task switch was considered a more direct test than RT reduction as recent work has demonstrated that ACC and pre-SMA activations do not necessarily correspond to the degree of behavioral conflict (Erickson et al., 2004; Lau et al., 2004; Ruff et al., 2001).

These parametric modulation values were determined separately for incongruent and neutral word reading. Thus, negative contrasts (−1) of each linear modulation parameter estimate identified all voxels that showed a decrease in activity for successive instances of word reading after a switch from color naming (see Henson et al., 2000 for a comparable approach to repetition priming). Using this methodology, only voxels that follow this modulated trajectory will reach significance. Inference was performed using a random effects analysis, thresholded at $P < 0.005$ voxel level ($t = 3.11$) for the parametric modulation ROI analyses in order to test our hypothesis about the specific pattern of a linear decline in activation with high sensitivity.

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