

Cognitive fatigue of executive processes: Interaction between interference resolution tasks

Jonas Persson, Kathryn M. Welsh, John Jonides, Patricia A. Reuter-Lorenz*

Department of Psychology, University of Michigan, East Hall, 530 Church Street, Ann Arbor, MI 48109-1109, USA

Received 23 May 2006; received in revised form 4 December 2006; accepted 5 December 2006

Abstract

A resource depletion framework motivated a novel strategy for investigating whether the central executive is unitary or separable into relatively independent subprocesses. The idea that tasks with overlapping neural representations may involve similar executive components was also critical to our approach. Of particular interest were tasks requiring resolution of interference among competing representations. Within a single experimental session intensive training *reduced* the ability to resolve interference on a transfer task if the training task placed high demands on interference resolution. Negative transfer was absent when interference resolution was minimally required by the task, or when the training and transfer tasks did not rely on overlapping neural representations. These results suggest a nonunitary central executive composed of separable subcomponents, at least one of which mediates interference resolution. Our results are consistent with an executive control process specialized for the selection of task-relevant representations from competitors. The results also agree with the view that higher cognitive processes are resource limited and can be temporarily depleted.

© 2006 Elsevier Ltd. All rights reserved.

Keywords: Prefrontal; Cognitive control; Semantic; Memory; Negative transfer; Working memory

Executive functions are mechanisms that control the content and progression of cognitive processes. Although some schemes originally conceptualized the central executive as a unitary entity (e.g., [Baddeley & Hitch, 1976](#); [Kimberg & Farah, 1993](#)), there is now considerable neuropsychological and neuroimaging evidence indicating that the central executive can be differentiated into several relatively independent functions (e.g. [Smith & Jonides, 1999](#)). While an established taxonomy is lacking, response inhibition, selective attention and task-switching are widely recognized as executive functions that control cognitive processes to achieve successful task completion. Recent neuroimaging work suggests that these functions may be localized in discrete parts of the prefrontal cortex (PFC). Moreover, different tasks designed to isolate specific executive processes engage common regions of localized activation (e.g., [Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997](#)). This evidence suggests that specific executive mechanisms entail fundamental and dis-

sociable processes that may be shared among different cognitive tasks.

If this interpretation of evidence for co-localized activity is correct, then executive processes may be susceptible to behavioral interactions between tasks. Such interactions could involve negative *or* positive transfer between tasks that are presumed to involve the same executive functions. Recent reports provide evidence for both types of transfer effects. For example, working memory ([Klingberg, Forssberg, & Westerberg, 2002](#)), inhibitory control ([Dowsett & Livesey, 2000](#)), and dual-task management ([Kramer, Larish, & Strayer, 1995](#)) can be *enhanced* by extensive training over days and weeks, and training effects can transfer to other tasks thought to involve similar executive processes. Conversely, intensive performance of one or more complex tasks involving multiple executive processes can subsequently result in *reduced* performance on other tasks presumably sharing these executive processes (e.g., [Van der Linden, Frese, & Meijman, 2003](#)). Such cognitively challenging tasks are presumed to cause cognitive fatigue or resource depletion (e.g., [Parasuraman, 1998](#); [Wickens, 1984](#)) thereby compromising performance on other tasks that require the same executive resources ([Engle, Conway, Tuholski, & Shisler, 1995](#); [Vohs & Heatherton, 2000](#)).

* Corresponding author. Tel.: +1 734 764 6577; fax: +1 734 763 7480.
E-mail address: parl@umich.edu (P.A. Reuter-Lorenz).

These demonstrations of between task interactions implicate shared executive processes as the source of that interaction. What is lacking, however, is evidence for transfer effects that target a discrete executive process. The occurrence of specific and selective transfer effects would provide new support for the separable nature of executive processes and valuable converging evidence that a particular executive process is utilized in different cognitive tasks. The current investigation leveraged existing neuroimaging evidence for the localization of specific executive functions to examine between task interactions, with the aim of demonstrating process-specific transfer effects. We reasoned that tasks that engage overlapping brain mechanisms should be susceptible to behavioral transfer effects that could enhance or reduce performance depending in part on the training regimen (e.g., Kinsbourne, 1980). Here we adopt a resource depletion framework (Engle et al., 1995; Muraven & Baumeister, 2000; Richeson et al., 2003; Vohs & Heatherton, 2000) and expect to find negative transfer due to intensive “training” performance within a single session. Note, that our approach is different from manipulations intended to produce general cognitive fatigue, in that we aim to target negative transfer to tasks that engage a specific executive process while leaving unaffected tasks that do not require that process, as well as other executive processes themselves.

Recent work from our lab (Jonides, Smith, Marschuetz, Koeppel, & Reuter-Lorenz, 1998; Nelson, Reuter-Lorenz, Sylvester, Jonides, & Smith, 2003; Persson et al., 2004) and others (e.g., Badre & Wagner, 2004) has focused on task conditions that require the resolution of interference among competing representations. Although interference resolution has been associated with activation in the left inferior frontal gyrus (IFG; Brodmann’s 44/45), the specific executive control process that mediates this effect is not currently known. One proposal, originally advanced by Thompson-Schill et al. (1997), is that left IFG mediates controlled selection whereby task-relevant representations are selected from among competing alternatives. Indeed, there is mounting evidence that interference in different task domains may be mediated by a general selection process localized within left IFG (e.g., Badre, Poldrack, Pare-Blagoiev, Inslar, & Wagner, 2005; Fletcher, Shallice, & Dolan, 2000; Jonides et al., 1998; Moss et al., 2005; Thompson-Schill et al., 1997). Following the logic outlined above, if the same neural mechanisms mediate interference resolution in different tasks, these tasks should be susceptible to behavioral transfer effects.

In a series of three experiments, we tested whether tasks from different cognitive domains recruit a common executive control process that mediates interference resolution (IR). Three main criteria were used to select our experimental tasks: (i) prior empirical work indicated a critical role for executive control processes in their completion, (ii) high and low interference versions of the same task could be created, and (iii) available neuroimaging evidence linked such manipulations of executive demand to localized activation in prefrontal cortex. Within our single-session design, we expected that intensive performance of a “training task” would produce *negative* transfer, and our aim was to demonstrate process-specific fatigue. If two tasks share

a common but limited executive resource then performing one task, referred to here as the training task, should temporarily fatigue or deplete this specific executive process thereby disadvantaging a second task that requires this same resource, referred to here as the “transfer task”. Conversely, no training effects should be observed if tasks rely on different executive functions because the resources necessary for the transfer task have not been compromised.

The first experiment used verb generation as the transfer task and item recognition with letters as the training task. These tasks activate overlapping regions within the left IFG and can be manipulated to create high and low IR conditions (Persson, Nelson, Jonides, & Reuter-Lorenz, 2006). Verb generation (Thompson-Schill et al., 1997), a semantic memory task, requires participants to generate an appropriate verb in response to a visually presented noun. In the high interference condition the nouns have multiple alternative responses (i.e., high selection demands), whereas in the low interference condition there is a single dominant response to the noun (i.e., low selection demands). The former condition has been associated with higher activity in left IFG (Persson et al., 2004; Thompson-Schill et al., 1997). Letter recognition, a verbal working memory task, entails the short term retention of four letters, followed by a probe letter that requires a yes or no recognition response. The high interference condition included trials in which participants must reject a probe that was a member of a target set on a previous, but not the current, trial. This kind of proactive interference (PI) has been associated with increased activation in left IFG (Jonides et al., 2000; Nelson et al., 2003). In the low PI condition current probes did not overlap with items on the previous two trials. We hypothesize that intensive performance of the working memory task with high PI will produce negative transfer that will impair performance on the many condition of the verb generation task while having minimal effects on the few condition. No negative transfer is expected when the low interference version of the working memory task is used as a training task.

1. Experiment 1

1.1. Methods

1.1.1. Participants

Forty-eight young adults (24 male; age range: 18–30 years) recruited from the University of Michigan community through posted advertisements, gave informed consent, were native English speakers and had normal or corrected to normal vision. Participants were randomly assigned to one of two groups: one received high interference working memory task training, and the other group received low interference working memory training. This investigation was approved by the University of Michigan Institutional Review Board.

1.1.2. Materials

The nouns for the verb generation task were obtained from previous studies that used the verb generation task (Barch, Braver, Sabb, & Noll, 2000; Thompson-Schill et al., 1997). In short, the words in the verb generation task were concrete nouns (Kucera-Francis frequency range from 0 to 591, median frequency = 32; word length range from 3 to 8, median 4), and the high and low interference nouns were based on verb generation data from two independent groups of subjects ($n = 30$ and 50 ; see Thompson-Schill et al., 1997 for a more detailed description).

1.2. Procedure

All experiments were performed in a dimly lit, sound attenuated room. Stimuli were presented on a 15-in. monitor, at a 50 cm viewing distance. E-PRIME software was used (Psychology Software Tools, Pittsburgh). For all experiments, a short practice session included both the training and transfer tasks. Each experiment consisted of three phases, with the first and last phase being the transfer task, and the intermediate phase being the training task (Fig. 1A).

In the transfer task of Experiment 1, participants were asked to generate silently a verb in response to a visually presented noun (see, Persson et al., 2004 for more details). The subjects were instructed to press the left mouse button when they had generated a verb. The nouns appeared for 3400 ms each and button responses were recorded during the presentation of the noun. The high interference condition (MANY) used nouns with several appropriate associated responses (e.g., BALL—THROW, KICK, BOUNCE) but which lacked a clear dominant response. In the low interference condition (FEW), nouns had one dominant response, or only a few associated responses (e.g., SCISSORS—CUT). Sixty-four nouns were presented in total; 32 were presented before the training phase and 32 were presented after the training phase. Each of the 32-item lists included 16 high and 16 low selection items presented in a random order. Participants were not informed of the existence of the high/low interference manipulation. In order to insure comparability between these results and previous fMRI findings, covert responses were used in the task. Previous data from our own lab using a voice key, however, show that the interference effect is similar for overt and covert responses (paired sample *t*-test; $t(14) = 1.92$, *ns*) and that the subjects are indeed generating verbs in correspondence to task instructions.

In the working memory task, used as the training task in Experiment 1, 144 trials were divided into three 48-trial blocks with a 1 min rest period between blocks. Each trial began with four lowercase letters and a central fixation cross presented in a square configuration for 1500 ms. A 1500 ms probe followed a 3000 ms delay and consisted of a single uppercase letter. On 50 percent of the trials, the probe was a member of the current target set, and on 50 percent of the trials it was not. Subjects responded “yes” for a match with their right index

finger, or “no” for a mismatch, with their right middle finger. The inter-trial interval was 1500 ms and there were no more than two consecutive positive or negative trials.

In the *low* interference condition, negative probes were neither members of the current target set nor in the target set of the previous two trials. In the *high* interference condition, one third of the negative probes were (i) neither in the current target set nor in the target set of the previous two trials (low interference), (ii) a letter in the previous target set, but not in the set before that (familiar), (iii) a letter in the previous two trials (highly familiar). Positive probes were non-overlapping with targets on the previous two trials and did not differ between the two training groups. For all subsequent analyses, trials with both familiar and highly familiar probes are considered high interference trials. The total time for the working memory tasks was approximately 18 min.

2. Results

For all analyses, in all experiments, subjects’ medians were used to minimize the effect of extreme values on the distribution. Test-retest performance on the verb generate task is shown in Table 1, where improvement in the speed of performance is generally evident between pre and post sessions. This improvement is presumably due to practice on verb generation, and is commensurate with practice effects we have observed on this task in other studies (Persson et al., 2004). In several prior data sets we have also observed a non-significant tendency for interference (estimated by the RT difference between MANY and FEW) to become reduced with practice at verb generation in the absence of any intervening tasks. We also note an apparent but non-significant baseline difference between the groups in the interference scores ($t = 1.34$, $P = .212$). The

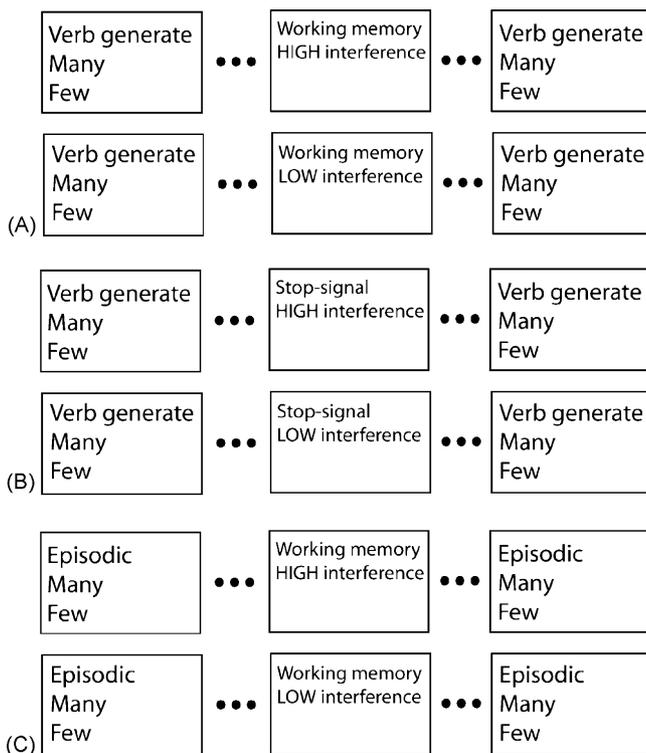


Fig. 1. Schematic depiction of the basic design of Experiments 1–3. From left to right, task administered before practice, practice task (high/low), and task administered after practice.

Table 1
Results from the transfer tasks for each of the experiments

Selection demand	Test phase	Group, median (SE)	
		Low	High
Experiment 1 (RT): verb generate–Sternberg–verb generate			
Few	Pre	989.56 (49.02)	990.35 (73.92)
	Post	879.79 (45.87)	921.85 (71.79)
Many	Pre	1180.94 (61.46)	1106.79 (73.42)
	Post	1028.02 (59.99)	1150.83 (93.96)
Experiment 2 (RT): verb generate–stop-signal–verb generate			
Few	Pre	938.46 (61.93)	1020.92 (54.08)
	Post	757.18 (48.35)	872.04 (43.33)
Many	Pre	1084.07 (73.06)	1240.30 (59.70)
	Post	891.67 (73.43)	1075.63 (61.70)
Proactive interference	Test phase	Group, median	
		Low	High
Experiment 3 (RT): episodic–Sternberg–episodic			
High	Pre	989.61 (35.27)	1093.03 (45.25)
	Post	931.66 (41.32)	944.77 (34.00)
Low	Pre	1159.17 (44.45)	1237.24 (51.45)
	Post	1037.16 (52.08)	1168.95 (61.45)
Experiment 3 (Accuracy): episodic–Sternberg–episodic			
High	Pre	12.31 (.376)	12.37 (.422)
	Post	12.13 (.347)	12.09 (.522)
Low	Pre	8.73 (.486)	9.49 (.484)
	Post	8.77 (.458)	8.93 (.518)

Table 2
Results from the training tasks for each of the experiments

Type	Group, RT/errors	
	Low	High
Exp1		
Yes trial	698.48/9 percent	646.90/7 percent
No trial (no fam)	713.98/5 percent	695.02/6 percent
No trial (fam1)		710.31/5 percent
No trial (fam2)		747.36/8 percent
Exp3		
Yes trial	686.88/9 percent	692.28/8 percent
No trial (no fam)	692.95/5 percent	724.96/5 percent
No trial (fam1)		732.83/10 percent
No trial (fam2)		806.97/10 percent

Exp1 = Sternberg as training task and verb generate as transfer task.
Exp3 = Sternberg as training task and Episodic PI as transfer task. Results from Experiment 2 are reported in text.

process-specific fatigue hypothesis predicts that the magnitude of pre-post differences will vary depending upon the specific processes that are engaged by the training and transfer tasks. It was therefore important to verify significant PI in the high interference version of the training task. For the transfer task, the interference was measured by subtracting the RTs for low interference trials from the RTs for high interference trials (i.e., MANY vs. FEW). These will be referred to as interference resolution or IR-scores. IR-scores pre and post training were then compared to determine whether or not transfer occurred for each group.

Data from the working memory task are shown in Table 2. To verify that the intended interference effect was present in the working memory performance of the HIGH interference group we examined the effect of PI using a one-way repeated measures ANOVA on response times to the NO trials with high familiarity compared to unfamiliar NO trials. This analysis showed a significant RT difference ($F(1, 23) = 8.33, P < .01$), indicating that subjects were slower on PI trials.

Second, to examine transfer effects on the ability to resolve interference in verb generation, we conducted a 2×2 (Group [high vs. low interference training] \times Time [Pre vs. Post] ANOVA on the IR-scores for each group (Fig. 2A). Only the Time \times Group interaction was significant ($F(1, 46) = 6.59, P < .05$). A planned comparison of the pre- and post IR-scores for the high interference group showed that the IR-scores increased after the training session ($t(23) = 2.16, P < .05$). The low interference group showed a non-significant trend in the opposite direction, which as noted above, we attribute to practice on verb generation per se.

The results reveal that the high interference group has a reduced ability (i.e., higher IR-scores) to resolve interference after the fatigue session compared to the low interference group. This result suggests high interference conditions of the working memory and verb generation tasks are mediated by a common, resource-limited cognitive mechanism. In order to establish the specificity of this mechanism, Experiment 2 paired the verb generation task with a different training task, the stop-signal task. The stop-signal task is known to involve executive control

processes, including response inhibition, although these have been localized to brain regions that do not overlap with regions associated with the interference resolution demands of verb generation and working memory (Aron, Robbins, & Poldrack, 2004).

2.1. Experiment 2

According to our hypothesis, if the executive processes recruited by two tasks rely on functionally and neurally separable mechanisms, then negative transfer between these tasks should be minimal. In this experiment we used a stop-signal task as the training task while using the semantic task from Experiment 1 as the transfer task. The stop-signal task entails the executive processes mediating response inhibition, which bears some conceptual resemblance with interference resolution, but has been associated with right, rather than left, inferior prefrontal function (Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003). Despite their reliance on prefrontal executive control mechanisms, we predict transfer between these tasks should be minimal because they recruit anatomically and functionally distinct executive processes. In particular, neither high nor low inhibition conditions in the training task should affect subjects' ability to meet the interference resolution demands of the transfer task (i.e., verb generation).

Two versions of the stop-signal task were used, one with a low proportion (20 percent) of stop-trials, and one with a high proportion (50 percent) of stop-trials. More frequent stop-trials have been associated with slower reaction times to the go stimulus and a decrease in the percentage of unsuccessful stops (i.e., commission errors). This suggests that subjects engage greater cognitive control, indicated by the longer RTs and fewer errors, in response to increased number of stops. Greater activation of right IFG, suggesting higher control demands, is found for successful compared to unsuccessful stops (Rubia, Smith, Brammer, & Taylor, 2003) and under conditions that increase response inhibition by increasing the delay between the go and the stop-signal (Brown & Braver, 2005).

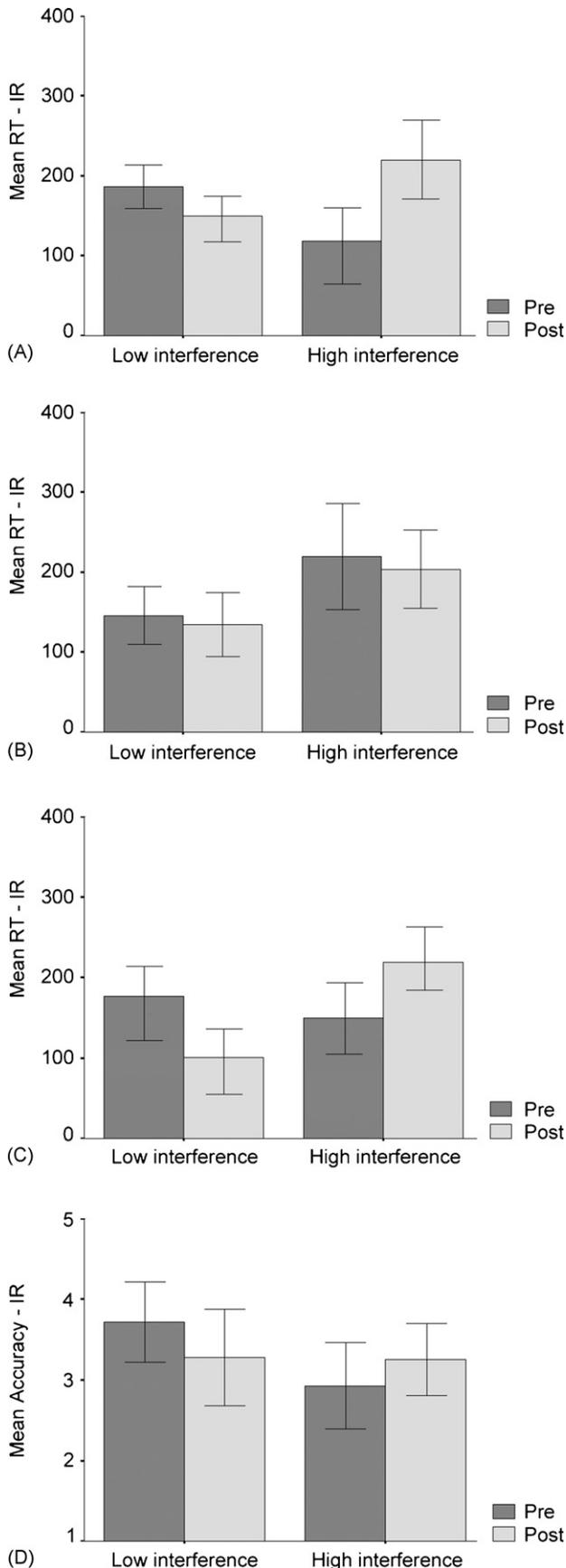
2.2. Methods

2.2.1. Participants

Forty-eight young adults (24 male; age range: 18–30 years) were recruited from the University of Michigan community through posted advertisements using the criteria described for Experiment 1. Participants were randomly assigned to either the *high* or *low* inhibition version of the stop-signal (training) task.

2.2.2. Procedure

The basic 3-phase procedure was the same as in Experiment 1 (Fig. 1B). In the stop-signal task, arrows (of 500 ms duration each) pointing either to the left or to the right side appeared at the center of a computer screen with an inter-stimulus interval of 1800 ms. Subjects were instructed to make a button response with their index finger or middle finger corresponding to the arrow direction. The arrows pointing left or right were followed unpredictably (600 ms later) by an arrow pointing upward. On these stop trials, subjects were instructed to withhold their responses. A total of 480 trials were presented in two blocks with 240 trials in each block, and the total time for this task was approximately 20 min.



3. Results

Test-retest performance on the verb generate task is shown in Table 1. The approach to data analysis is similar to Experiment 1, including the calculation of the IR-scores.

First, analysis of the stop-signal data showed that the high inhibition group performed more accurately than the low inhibition group (percentage unsuccessful stop trials [high inhibition = 9 percent, low inhibition = 26 percent]; $t(46) = -2.17, P < .05$). The high inhibition group also had longer RTs (567 ms) on GO trials than the low inhibition group (407 ms); this difference was significant with a one-tailed test ($t(46) = 1.69, P < .05$). These results suggest that the high inhibition group was more cautious, and presumably engaging in response inhibition processes to contend with a greater number of STOP trials. Since it has been suggested that inhibition during a STOP trial may influence the subsequent GO response time (i.e., after-effects; Rieger & Gauggel, 1999) we analyzed the data by dividing the GO trials based on whether the preceding ($n - 1$) trial was a STOP or GO trial. We did not find any differences between these two categories of GO trials ($F(1) = 1.21, P = .298$) suggesting minimal after-effects. When the preceding trial type was taken into consideration in the between-group analyses, we found a significant group difference for GO trials that were preceded by a GO trial ($t(46) = 2.12, P < .05$). When the GO trial was preceded by a STOP trial the group difference was non-significant, but showed a trend ($t(46) = 1.43, P = .066$, one-tailed) suggesting longer RTs for the HIGH inhibition group even if the preceding trial was a STOP. Importantly, the high inhibition group performed more accurately than the low inhibition group (percentage unsuccessful STOP trials) independent of whether the preceding trial was a STOP or GO. Although the RT data suggests that after-effects may have influenced the results, the effect appears to be small.

Second, we conducted a 2×2 (Group [high vs. low inhibition training] \times Time [Pre vs. Post] ANOVA on the IR-scores to test for transfer between the stop-signal and the verb generation tasks (Fig. 2B). The results showed no main effects, and no Group \times Time interaction ($F < 1, ns$), suggesting that the stop-signal task did not affect the ability to select among competing alternatives in the subsequent semantic task. Once again any baseline differences between the groups for the MANY and FEW conditions, and for the IR-scores, were all non-significant (MANY: $t(46) = 1.55, P = .120$; FEW: $t(46) = 1.21, P = .232$; IR-scores: $t = 1.01, P = .319$).

3.1. Experiment 3

Experiment 3 was intended to replicate and extend the findings from Experiment 1 using a transfer task that relies

Fig. 2. Mean interference resolution scores (reaction time and accuracy), as a function of group (high/low interference), and time (before/after practice). (A) Experiment 1—Sternberg as practice task and verb generate as transfer task, (B) Experiment 2—Stop-signal as practice task and verb generate as transfer task, and (C) Experiment 3—Sternberg as practice task and Episodic PI as transfer task (RTs) and (D) correct responses. IR = interference resolution score (difference in RT/Accuracy between high and low interference resolution trials (A–C = milliseconds; D = correct remembered trials).

on a different memory system. We selected a verbal episodic memory task in which the degree of PI could be manipulated. As in the domain of working memory, subjects typically respond more slowly and with more frequent errors on episodic memory conditions with high PI (for a review, see Anderson & Neely, 1996). Similar to semantic and working memory conditions with high interference, proactive interference trials in the episodic task may engage selection processes for successful task execution. Moreover, there appears to be some anatomical overlap in the neural substrates recruited by working memory and episodic memory tasks in that recent neuroimaging studies show similar left inferior frontal activations during high interference trials in both tasks (Henson, Shallice, Josephs, & Dolan, 2002; Jonides et al., 1998; Nelson et al., 2003). In the present experiment, the episodic memory task served as the transfer task, and the high and low interference versions of the working memory task again served as the training tasks (Fig. 1C). Similar to Experiment 1, we hypothesized that high interference training would result in reduced ability to resolve interference (i.e., process-specific fatigue) on the transfer task compared to low interference training.

3.2. Methods

3.2.1. Participants

Eighty-eight young adults (31 male; age range: 18–30 years) were recruited and met the inclusion criteria as in the prior experiments. Participants were randomly assigned to either the high or low interference training group.

3.2.2. Materials

The episodic task used paired associates. For 64 common nouns the three most frequent associates were generated from the Edinburgh Associative Thesaurus (<http://www.itd.clrc.ac.uk/Activity/Psych+267>). For each subject, four blocks of eight word-associate sets were presented before and after training.

3.2.3. Procedure

Phases 1 and 3 consisted of the episodic memory transfer task, and phase 2 was training on letter recognition (Fig. 1C). Each block of the episodic task consisted of a study phase and a test phase. During the study phase, a cue and its associate were displayed simultaneously for 3 s, with a fixation cross presented during the inter-stimulus interval. The word pairs were presented three times, with high and low interference conditions randomly intermixed. Participants were told that some of the cue words would be repeated but with different associates (e.g., QUEEN–KING; QUEEN–BEE; QUEEN–CROWN), whereas others would be repeated with the same associate. They were also told that, during a subsequent memory test, the cue would be presented and they would have to recall the most *recent* associate. For the high interference condition, the cue was paired with a different associate each time, and in the low interference condition, it was paired repeatedly with the same associate. Subjects were instructed to respond as fast and accurately as possible.

During the test phase, a cue word was displayed for 4 s and the subjects were instructed to retrieve the most recent associate of that cue word from the study phase. For 64 of the subjects (32 in the high and 32 in the low interference groups, respectively), the cue word was presented twice. First, subjects were given the cue word with the subsequent visual command “press!” and subjects were instructed to press with their index finger when they have generated the associate for a given cue word. Second, the visual command “speak!” followed the presentation of the cue word at which point the subjects were instructed to articulate the response. Response times were recorded using a computer mouse, and verbal responses were collected on the computer using a microphone. In an effort to improve sensitivity of the response time measure, 24 of the subjects (12 in the high and 12 in the low interference groups, respectively) used a voice key. These subjects were presented with a cue word for 4 s and instructed to retrieve and overtly articulate the most recent associate of that cue from the study

phase. All subjects were instructed to say “pass” if they could not remember the associate. Cues corresponding to the high and low interference condition were randomly intermixed. Response times were recorded using the voice key, and verbal responses were collected on the computer using a microphone, and subsequently transcribed and scored for accuracy.

4. Results

Test-retest performance on the episodic task is shown in Table 1. Data from the working memory task are shown in Table 2. Response time was calculated for correct responses only. The approach to data analysis is similar to Experiments 1 and 2. For the transfer task, the effect of interference was calculated by subtracting the RTs for low interference trials from the RTs for high interference trials (i.e., high PI vs. low PI). Similarly, the interference effect for accuracy (expressed as the number of correct trials out of a maximum of 16 correct trials) was calculated by subtracting accuracy for low interference trials from high interference trials (i.e., low PI vs. high PI). These scores will be referred to as IR-scores.

We confirmed the presence of PI for the high interference group using a one-way repeated measures ANOVA to compare the RTs to familiar and unfamiliar NO trials. Subjects were slower on familiar trials indicating a significant interference effect ($F(1, 42) = 49.9, P < .001$).

Next, we examined transfer effects by comparing IR-scores before and after the working memory task for the two groups using a 2×2 (Group [high vs. low interference training] \times Time [Pre vs. Post] ANOVA (Fig. 2C). Only the Time \times Group interaction was significant ($F(1, 84) = 4.03, P < .05$). A planned comparison of the pre- and post IR-scores for the high interference group showed that the IR-scores increased after the training session ($t(43) = 1.50, P < .05$, one-tailed). Together these results indicate that the high interference group has a reduced ability (i.e., higher IR-scores) to resolve interference after the training session. This result confirms the finding from Experiment 1, and suggests that interference resolution in the training and transfer tasks is mediated by a common, resource-limited cognitive mechanism.

In order to examine whether the response mode (i.e., voice key vs. button press) yielded any difference in the effect of fatigue and interference resolution we also used response mode as a factor in the analysis of fatigue effects. The Time \times Group \times Response mode (button press vs. voice key) interaction was not significant ($F(1, 83) < 1$).

We also examined transfer effects on accuracy by conducting a 2×2 (Group [high vs. low interference training] \times Time [Pre vs. Post] ANOVA on the accuracy IR-scores to examine the effects of the training session on the respective groups. For this analysis, the interaction did not reach significance ($F(1, 84) = 0.49, P > .10$), although the means were in the predicted direction.

5. Discussion

In this investigation, we tested the hypothesis that interference resolution is mediated by a separable executive process that

is shared by tasks in different cognitive domains. Our goal was to provide converging behavioral evidence to complement the existing neuroimaging data suggesting that these tasks share a common neural substrate. The process-specific fatigue effects demonstrated between pairs of tasks, provides behavioral support for their reliance on a common mechanism. In particular, the results showed that performing a working memory task with high interference trials resulted in reduced ability to resolve interference in both a semantic task and an episodic task. In contrast, participants who trained on a working memory task without interference had no reduction in the ability to resolve interference on the transfer tasks. When two tasks that did not involve the same executive demands (response inhibition vs. interference resolution) were used, neither version of the training task had any effect on the transfer task. This pattern of results was predicted based on neuroimaging evidence indicating anatomical overlap, or lack thereof, between the neural circuitry recruited by the executive demands in these tasks. The current observations suggest that tasks used to investigate performance in several different cognitive domains (episodic memory, working memory, and semantic memory) share a common executive component. Furthermore, this component can also be separated from other specific executive functions, such as response inhibition.

These conclusions are generally consistent with studies using latent variable techniques to investigate whether the central executive is unitary or can be separated into several partially independent mechanisms. For example, using a large sample of subjects, Miyake et al. (2000) investigated several tasks that required executive processes in order to determine the separability of three putative executive functions (shifting, updating and inhibition). Using confirmatory factor analysis they found that these three executive components are correlated with each other, but are clearly separable, indicating both unity and diversity of executive functions. Another common finding, however, is that intercorrelations among widely used executive tasks can be low and lack statistical significance (e.g., Lehto, 1996), as one might expect if the tasks draw on separable executive functions.

Although the exact properties of the mechanism(s) recruited in the present high interference conditions remain to be specified, our findings provide some constraints on the nature of the shared executive process and have implications for the functional organization of IFG. First, as mentioned above, the lack of an interaction between the verb generate task and the stop-signal task in experiment two dissociates interference resolution demands from response conflict or inhibition, an outcome that is consistent with prior work from our lab (Nelson et al., 2003) and others (see e.g., Aron et al., 2004). Second, while there may be greater demands on context retrieval operations in the high PI conditions of the working memory and episodic memory tasks (e.g., Badre & Wagner, 2004), there is no apparent need for context retrieval in the high interference condition of verb generation. Therefore context retrieval does not provide a satisfactory description of a control process that might be shared by all three tasks. Another process attributed to subregions of IFG is controlled memory retrieval, which refers to the engagement of top-down retrieval operations when more automatic processes (i.e., familiarity, associative strength) are insufficient to guide

responses (e.g., Badre & Wagner, 2004). Although it could be argued that the high interference conditions of all three tasks involve controlled retrieval, the source from which information is retrieved clearly differs between the tasks in that verb generation draws from semantic memory, the paired-associates task from episodic memory, and the letter identification task presumably draws from working memory. Moreover, controlled semantic retrieval has been linked to left BA 47 which is anterior (e.g., Gold, Balota, Kirchoff, & Buckner, 2005; Poldrack et al., 1999) to the 44/45 region that is commonly activated by the three interacting tasks in the present study.

We believe the most satisfying account of the present results is the possibility of a general selection process that is engaged when goal-relevant representations must be selected from among competitors (Badre et al., 2005). A general selection process that is recruited to meet the demands imposed by competing representations would provide a unitary account of the interactions we observe among the three high interference conditions in the present set of studies. Importantly, a selection process can be involved in multiple memory and task domains if this mechanism operates on active representations that are maintained in working memory. Thus, the general selection processes implicated here could potentially be involved in a range of tasks that extends beyond those used in the current study. One potential operation that could implement selection is an attentional template that consists of properties relevant for the current task (see Jonides & Nee, 2006 for a discussion). The particular properties of the template, and the representations on which it acts would be determined by the dynamic interplay between the shared neuroanatomical resource and task specific circuitry that could presumably be identified via connectivity analyses applied to neuroimaging data.

The results from these experiments support a resource model of executive processes. Some evidence for resource depletion of executive functions (i.e., negative transfer) more generally has been found in studies of suppression of stereotypes and negative attitudes and self-regulation (e.g., Richeson et al., 2003; Vohs & Heatherton, 2000). Neural correlates of resource depletion related fatigue effects have also been observed in lower-level systems. For example, reduced functional activation of primary motor cortex has been found following fatiguing exercise of the hand (Benwell et al., 2006). Furthermore, prolonged exposure to a visual pattern disturbs visual perception, and single cell recording show have shown that prolonged stimulation of about 30 s fatigues visual neurons in the primary visual cortex to give a weaker response than they otherwise would (Carandini, 2000). However, the current study is, to our knowledge, the first attempt to use a resource depletion framework to examine a specific executive control process. Whether practice or experience involving executive function is transferred as reduced (i.e., fatigue) or enhanced (i.e., training) performance on a subsequent executive task is a question requiring further investigation. The answer appears to be related to a number of factors, including the extent of practice, and whether time is allowed for recovery.

It might be argued that selection processes, of the type the present experiments were designed to tap, may be active at some level in many everyday activities and therefore very resilient

to fatigue effects. It should be noted, however, that the effects of fatigue on selection processes are rather small and do not result in the inability for an individual to perform the task. A slight increase in RT to perform a certain cognitive operation in everyday life activities due to cognitive fatigue may not be recognizable if not specifically tested in an experimental setting. Also, even if an individual is engaged in a task that involves a specific executive component, everyday activities (e.g., a conversation) often allow for recovery, unlike the continuous engagement of selection processes in the present experiments.

The reliance of the stop-signal task to test to inhibition effects on subsequent selection processes may have some limitations. For example, longer RTs in the HIGH inhibition group compared to the LOW inhibition group could reflect a tendency to wait for the stop-signal in spite of instructions, instead of inhibitory processes. With the current design, the interpretation that participants in the HIGH inhibition group change their decision criteria in response to the increased number of stop-trials cannot be completely ruled out.

In conclusion, the current data extend prior neuroimaging evidence for executive processes that are shared across cognitive domains by demonstrating behavioral interactions between tasks hypothesized to recruit the same process. These observations support a nonunitary central executive composed of separable subcomponents, one of which may be a general selection mechanism that resolves interference. The results also agree with the view that cognitive control processes are resource limited and can be temporarily depleted.

Acknowledgments

We would like to thank Sharon Thompson-Shill and Deanna Barch for providing us with stimulus material for the verb generation task. This work was supported by the National Institutes of Health Grant AG18286.

References

- Anderson, M. C., & Neely, J. H. (1996). Interference and inhibition in memory retrieval. In E. L. Bjork & R. A. Bjork (Eds.), *Memory: Handbook of perception and cognition* (pp. 237–313). San Diego, CA: Academic Press.
- Aron, A. R., Fletcher, P. C., Bullmore, E. T., Sahakian, B. J., & Robbins, T. W. (2003). Stop-signal inhibition disrupted by damage to right inferior frontal gyrus in humans. *Nature Neuroscience*, *6*, 115–116.
- Aron, A. R., Robbins, T. W., & Poldrack, R. A. (2004). Inhibition and the right inferior frontal cortex. *Trends in Cognitive Sciences*, *8*, 170–177.
- Baddeley, A. D., & Hitch, G. J. (1976). Verbal reasoning and working memory. *Quarterly Journal of Experimental Psychology*, *28*, 603–621.
- Badre, D., Poldrack, R. A., Pare-Blagoev, E. J., Insler, R. Z., & Wagner, A. D. (2005). Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. *Neuron*, *47*(6), 907–918.
- Badre, D., & Wagner, A. D. (2004). Selection, integration, and conflict monitoring: Assessing the nature and generality of prefrontal cognitive control mechanisms. *Neuron*, *41*(3), 473–487.
- Barch, D. M., Braver, T. S., Sabb, F. W., & Noll, D. C. (2000). Anterior cingulate and the monitoring of response conflict: Evidence from an fMRI study of overt verb generation. *Journal of Cognitive Neuroscience*, *12*, 298–305.
- Benwell, N. M., Sacco, M. L., Hammond, G. R., Byrnes, M. L., Mastaglia, F. L., & Thickbroom, G. W. (2006). Short-interval cortical inhibition and corticomotor excitability with fatiguing hand exercise: A central adaptation to fatigue? *Experimental Brain Research*, *170*, 191–198.
- Brown, J. W., & Braver, T. S. (2005). Learned predictions of error likelihood in anterior cingulate cortex. *Science*, *307*, 1118–1121.
- Carandini, M. (2000). Visual cortex: Fatigue and adaptation. *Current Biology*, *10*, 605–607.
- Dowsett, S. M., & Livesey, D. J. (2000). The development of inhibitory control in preschool children: Effects of “executive skills” training. *Developmental Psychobiology*, *36*, 161–174.
- Engle, R. W., Conway, A. R. A., Tuholski, S. W., & Shisler, R. J. (1995). A resource account of inhibition. *Psychological Science*, *6*, 122–125.
- Fletcher, P. C., Shallice, T., & Dolan, R. J. (2000). Sculpting the response space—an account of left prefrontal activation at encoding. *NeuroImage*, *12*(4), 404–417.
- Gold, B. T., Balota, D. A., Kirchoff, B. A., & Buckner, R. L. (2005). Common and dissociable activation patterns associated with controlled semantic and phonological processing: Evidence from fMRI adaptation. *Cerebral Cortex*, *15*(9), 1438–1450.
- Henson, R. N. A., Shallice, T., Josephs, O., & Dolan, N. J. (2002). Functional magnetic resonance imaging of proactive interference during spoken cued recall. *NeuroImage*, *17*, 543–558.
- Jonides, J., Marshuetz, C., Smith, E. E., Reuter-Lorenz, P. A., Koeppe, R. A., & Hartley, A. (2000). Age differences in behavior and PET activation reveal differences in interference resolution in verbal working memory. *Journal of Cognitive Neuroscience*, *12*(1), 188–196.
- Jonides, J., & Nee, D. E. (2006). Brain mechanisms of proactive interference in working memory. *Neuroscience*, *139*(1), 181–193.
- Jonides, J., Smith, E. E., Marshuetz, C., Koeppe, R. A., & Reuter-Lorenz, P. (1998). Inhibition in verbal working memory revealed by brain activation. *Proceedings of the National Academy of Science in the USA*, *95*(14), 8410–8413.
- Kimberg, D. Y., & Farah, M. J. (1993). A unified account of cognitive impairments following frontal lobe damage: The role of working memory in complex, organized behavior. *Journal of Experimental Psychology: General*, *122*(4), 411–428.
- Kinsbourne, M. (1980). Mapping a behavioral cerebral space. *International Journal of Neuroscience*, *11*, 45–50.
- Klingberg, T., Forssberg, H., & Westerberg, H. (2002). Training of working memory in children with ADHD. *Journal of Clinical and Experimental Neuropsychology*, *24*(6), 781–791.
- Kramer, A. F., Larish, J. F., & Strayer, D. L. (1995). Training for attentional control in dual-task settings - a comparison of young and old adults. *Journal of Experimental Psychology: Applied*, *1*, 50–76.
- Lehto, J. (1996). Are executive functions tests dependent on working memory capacity? *Quarterly Journal of Experimental Psychology*, *49A*, 29–50.
- Miyake, A., Friedman, N. P., Emerson, M. J., Witzki, A. H., Howerter, A., & Wager, T. D. (2000). The unity and diversity of executive functions and their contributions to complex “frontal lobe” tasks: A latent variable. *Cognitive Psychology*, *41*(1), 49–100.
- Moss, H. E., Abdallah, S., Fletcher, P., Bright, P., Pilgrim, L., Acres, K., et al. (2005). Selecting among competing alternatives: Selection and retrieval in the left inferior frontal gyrus. *Cerebral Cortex*, *15*(11), 1723–1735.
- Muraven, M., & Baumeister, R. F. (2000). Self-regulation and depletion of limited resources: Does self-control resemble a muscle? *Psychonomic Bulletin & Review*, *126*(2), 247–259.
- Nelson, J. K., Reuter-Lorenz, P. A., Sylvester, C.-Y. C., Jonides, J., & Smith, A. D. (2003). Dissociable neural mechanisms underlying response-based and familiarity-based conflict in working memory. *Proceedings of the National Academy of Science in the USA*, *100*(19), 11171–11175.
- Parasuraman, R. (Ed.). (1998). *The attentive brain*. Cambridge: MIT Press.
- Persson, J., Nelson, J. K., Jonides, J., Reuter-Lorenz, P. A. (2006). *Behavioral and neuroanatomical evidence for a core executive function: The case of interference resolution*. Paper presented at the Cognitive Neuroscience Society, San Francisco.
- Persson, J., Sylvester, C.-Y. C., Nelson, J. K., Welsh, K. M., Jonides, J., & Reuter-Lorenz, P. A. (2004). Selection requirements during verb generation: Differential recruitment in older and younger adults. *NeuroImage*, *23*, 1382–1390.

- Poldrack, R. A., Wagner, A. D., Prull, M. W., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1999). Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *Neuroimage*, *10*, 15–35.
- Richeson, J. A., Baird, A. A., Gordon, H. L., Heatherton, T. F., Wyland, C. L., Trawalter, S., et al. (2003). An fMRI investigation of the impact of interracial contact on executive function. *Nature Neuroscience*, *6*, 1323–1328.
- Rieger, M., & Gauggel, M. (1999). Inhibitory after-effects in the stop-signal paradigm. *British Journal of Psychology*, *90*, 509–518.
- Rubia, K., Smith, A. B., Brammer, M. J., & Taylor, E. (2003). Right inferior prefrontal cortex mediates response inhibition while mesial prefrontal cortex is responsible for error detection. *Neuroimage*, *20*, 351–358.
- Smith, E. E., & Jonides, J. (1999). Storage and executive processes in the frontal lobes. *Science*, *283*, 1657–1661.
- Thompson-Schill, S. L., D’Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proceedings of the National Academy of Science in the USA*, *94*, 14792–14797.
- Van der Linden, D., Frese, M., & Meijman, T. F. (2003). Mental fatigue and the control of cognitive processes: Effects on preservation and planning. *Acta Psychologica*, *113*, 45–65.
- Vohs, K. D., & Heatherton, T. F. (2000). Self-regulatory failure: A resource-depletion approach. *Psychological Science*, *11*, 249–254.
- Wickens, C. D. (1984). Processing resources in attention. In R. Parasuraman (Ed.), *Varieties of attention*. Florida: Academic Press.