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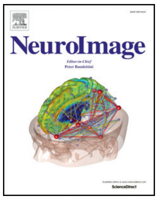

Modulating rest-break length induces differential recruitment of automatic and controlled attentional processes upon task reengagement

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ABSTRACT

Rest breaks are commonly administered as a countermeasure to reduce on-the-job fatigue, both physical and mental. However, this practice makes the assumption that recovery from fatigue, as measured by the reversal of performance declines, is the sole effect of taking a break on behavior. Here, through administering rest breaks of differing lengths in between blocks of a mentally demanding symbol decoding task, we show that this assumption may not be strictly true. First, we replicate previous work by showing that taking a longer break leads to two correlated effects: greater immediate rebound in performance, and greater subsequent time-on-task decline. Using fMRI, we reveal that time-on-task in this paradigm is associated with increasing recruitment of fronto-parietal areas associated with top-down control, and decreasing deactivation in the default-mode network. Finally, by analyzing individual differences, we reveal a potential neural basis for our behavioral observation: greater recovery following long breaks is associated with greater activity in the putamen, an area associated with the automatic generation of motor responses, followed by greater activity in left middle frontal gyrus by the end of those task periods. Taken together, this suggests a shift in the implicit engagement of automatic and controlled attentional processing following longer breaks. This shift may be undesirable or detrimental in real-world situations where maintaining a stable level of attention over time is necessary.

Introduction

Fatigue in the workplace is a serious but preventable cause of lapses, errors, and accidents (Landrigan et al., 2004; Williamson et al., 2011). Consequently, detecting and reversing its detrimental effects has been the subject of much ongoing investigation. One important focus of this research has been the impact of rest breaks and task interruptions on fatigue, work performance, and accident risk, with many studies finding a positive effect of rest on all of these variables (Tucker, 2003). The commonsense model, therefore, is that work and rest are two sides of the same coin, and that the processes associated with recovery are trivially a reversal of those associated with decline.

This assumption is implicit in the neuroergonomics literature (Parasuraman and Rizzo, 2008), in which the effects of mental fatigue but not recovery on human brain function have been well documented. One of the most robust findings in this field is that mental fatigue is associated with dysfunction in top-down executive control, and decreases in activity in associated areas (Paus et al., 1997; Coull et al., 1998; Boksem et al., 2005; Lim et al., 2010; Breckel et al., 2013; Langner and Eickhoff, 2013; Sun et al., 2014a). Specifically, these studies have shown that the integrity of the frontoparietal network is compromised with increasing time-on-task (TOT), leading to the failure of sub-processes such as goal maintenance, and target-driven reorientation of attention. The amplitude of event-related potential (ERP) components associated with error monitoring and inhibition is also significantly reduced as a person enters a state of fatigue (Boksem et al., 2005; Lorist et al., 2005). Using individual differences analysis, it has been shown that failure to maintain good performance occurs *in spite of* compensatory top-down effort, and not for want of it (Bonnefond et al., 2010; Demeter et al., 2011). In short, a fairly comprehensive picture of the brain under conditions of fatigue has emerged from these investigations.

In contrast, the cognitive neuroscience of mid-tasks breaks has been almost completely ignored. This is in part due to intuitions drawn from resource theory (Warm et al., 2008) that rest breaks simply reverse the neural effects observed over periods of fatigue by releasing demands on cognitive and neural resources, putatively allowing them to be replenished (Helton and Russell, 2012). However, recent work on this subject suggests that a more nuanced view might be warranted. For example, Lim et al. (2013) reported that there are substantial individual differences in the degree of recovery received during a rest period, with spectral power in the upper alpha (10–12 Hz) band of electroencephalographic activity predicting improvements in reaction time following a break. Helton and Russell (2015) reported that the specific activity performed during a break is an important moderator of how much recovery it affords. Finally, Lim and Kwok (in press) recently demonstrated that the immediate recovery observed after a break is

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inversely correlated with the time-on-task slope in the subsequent work block. This last behavioral finding prompted us to set up the current replication study, as well as interrogate the neural correlates of this novel effect.

To this end, we used fMRI to study brain activation in a test of cognitive throughput interspersed with breaks of different lengths. This test was self-paced; that is, participants determined the rate at which they worked, as opposed to the task having a pre-determined event rate. We hypothesized that we would replicate our previous behavioral findings: that the immediate recovery received from a break correlates with the slope of time-on-task in the succeeding task block. Furthermore, we predicted that higher levels of prefrontal activation would accompany greater TOT declines in the blocks following longer breaks, indicating the increased engagement of executive attention.

Methods

Participants

Participants were recruited from the National University of Singapore through online advertising and word-of-mouth. All participants were screened for right-handedness (Oldfield, 1971) and normal or corrected-to-normal vision, and to ensure they had no history of long-term physical or psychological disorders. Eligible individuals were invited for a behavioral screening session ($N = 31$), and those who achieved performance criterion during this session were invited for the fMRI session approximately one week later ($N = 30$). Of these, 1 participant dropped out prior to the fMRI session, and 2 were eventually excluded for excessive head motion in the scanner, yielding a final sample size of 27 (12 male; mean (SD) age = 22.7 (1.74)).

Blocked Symbol Decoding Task (BSDT)

To measure the effects of variable rest pauses on a self-paced task, we used a modified symbol-decoding task similar to the Symbol-Digit Modality Test (Smith, 1982) (Fig. 1). Participants learned a mapping of four symbols ('⊥' '+' '×' 'Λ') to four letters ('f' 'g' 'h' 'j'), and were required to press the appropriate letter key (on a standard QWERTY keyboard) with their right hand when each symbol appeared. Each self-paced trial consisted of one symbol presented at a time in the centre of the screen, at approximately 1 degree of visual angle. This symbol was replaced immediately by the subsequent symbol following a response. Consecutive stimuli were always different. Each block of the BSDT consisted of 150 trials, followed by a pseudorandom, predetermined rest break of either 12 s or 28 s. Stimuli were presented using Psychtoolbox (Brainard, 1997; Pelli, 1997), via MATLAB R2012A (http://www.mathworks.com).

Procedure

All testing took place in the Cognitive Neuroscience Laboratory of the Duke-NUS Graduate Medical School, and all testing sessions were held between 1:00 and 4:00 pm to control for possible circadian confounds. The first session was a behavioral screening session, which was administered to minimize practice effects during the fMRI scanning session, as well as to exclude very slow responders, due to the time limitations of the fMRI scan.

During this screening session, participants were first instructed on how to perform the BSDT, and underwent two practice runs. In the first practice run, participants were shown a legend mapping the symbols to the appropriate letters. They performed 600 trials in this first practice run to learn the mapping of the symbols to the letters. In the second practice run, participants performed 150 trials of the same task, with the legend removed. In the second practice run, participants received feedback if they made an incorrect response. Following these two practice runs, participants underwent two experimental runs consisting of 7 task blocks interleaved with 6 rest breaks. A 5-minute rest opportunity was provided between the two runs. We excluded participants who did not achieve at least 90% accuracy during the two experimental runs, and or had median reaction times of >1000 ms (>3 SD than median RT of the sample).

Participants who achieved criterion in the screening session were invited for fMRI scanning on a separate day approximately one week later. They were asked to refrain from alcohol and caffeine for 6 h prior to arrival for scanning. On arrival at the center, participants performed a two-block practice run before the fMRI scan as a reminder of the task procedure. They were then given a 30-minute rest opportunity before entering the scanner. fMRI scans were collected in the following order: resting-state fMRI (~8 min), BSDT, high-resolution MPRAGE, BSDT, and resting-state fMRI. Data from resting-state fMRI scans are not reported in this paper.

In the scanner, BSDT stimuli were projected onto a screen using an LCD projector, and participants viewed these through a mirror positioned at their eye level inside the head coil. Participants responded

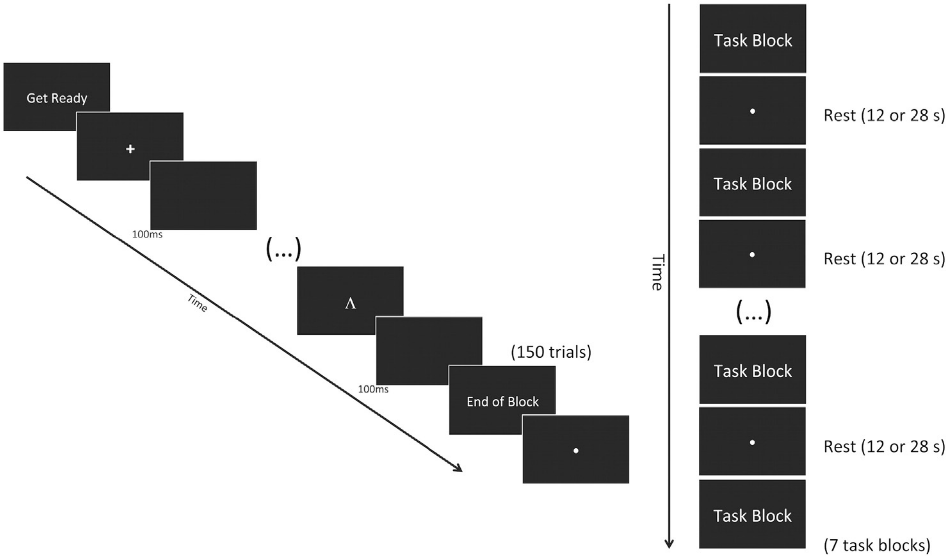

Fig. 1. Experimental paradigm. Participants performed the Blocked Symbol Decoding Task (BSDT). Left: each task block consisted of 150 decoding trials. Right: Participants performed 7 blocks of the task in each run. Blocks were separated by break periods of either 12 s or 28 s, in a pseudo-random, predetermined order.

using their right hand with a four-button MR-compatible button box (Current Designs, Philadelphia, PA). The position of the buttons that were mapped to each symbol corresponded to the positions of the letter keys on the QWERTY keyboard. Each experimental run in the fMRI session consisted of seven blocks of the BSDT with interleaved rest breaks, and participants completed two runs in total (mean run length = 14 min 37 s; SD = 2 min 23 s). Participants were given a 5-minute rest opportunity between these run to recover to their baseline level of performance, during which the high-resolution anatomical scan was acquired. The entire task protocol lasted approximately 1 h.

The protocol for this study was approved by the Institutional Review Board of the National University of Singapore, and all participants provided written informed consent prior to the experiment. Participants were compensated S$10.00 (Singapore dollars) for their time in the practice session, and S$40.00 for the fMRI session, for a total payment of S$50.00.

fMRI data acquisition

Functional imaging was conducted on a Siemens 3T MAGNETOM Prisma scanner (Siemens, Erlangen, Germany) using an interleaved echo-planar imaging (EPI) sequence (TR: 2000 ms; TE: 30 ms; flip angle: 90°; field-of-view: 192 × 192 mm; matrix size: 64 × 64). 36 3.5-mm oblique axial slices aligned to the intercommissural plane were acquired for all functional runs. A T1-weighted high-resolution 3D-MPRAGE (1 mm × 1 mm × 1 mm) sequence (TR: 2300 ms; TE: 2.28 ms; TI = 900 ms; flip angle = 8°**;** field-of-view: 256 × 240 mm; BW = 240 Hz/Px; matrix size: 256 × 240, voxel size: 1 mm^3; 192 slices) was performed between the two functional runs.

Behavioral data analysis

In agreement with previous studies of speeded, self-paced tasks, we observed that all participants experienced "mental blocking" (Bills, 1931; Broadbent, 1953), which manifested as a small number (mean = 10.85, SD = 4.22; or 0.05% of responses) of extremely slow responses (RT > 5 SD, relative to mean RT). These were removed from the data before further behavioral analysis.

Following outlier removal, we used a linear fit to estimate the trend of change in response time within each task block for each individual subject. Data were first smoothed by applying a sliding window over the time series of RTs to obtain average RTs over sets of 20 responses. These averages ($N = 131$) were regressed against the number of the window within each block to obtain three variables: a slope value, an intercept value (predicted RT at the start of the block), and a predicted RT for the end of the block. This approach is very similar to our previously reported method of analysis (Lim and Kwok, in press).

We interrogated the effect of the varying break lengths using two measures: 1) the relative change from predicted RT at the end of the pre-break block to the intercept of the post-break block, and 2) the slope in the post-break block. Variable #1 was subsequently used as a between-subjects covariate in modeling the fMRI data (see *fMRI data analysis*). We focused on the effect of RTs over accuracy in this analysis for consistency with our previous reports (Lim et al., 2013; Lim and Kwok, in press), and because accuracy did not show declines over time that were as clear as in the RT data (Supplementary Figure 1).

fMRI data analysis

fMRI analysis was performed using FSL Version 5.0.8 (FMRIB Software Library, (Jenkinson et al., 2012), with visualization of results using MRIcron (Rorden and Brett, 2000). Data were skull-stripped using BET. Preprocessing was carried out by discarding the first two volumes of the functional time series, correcting for interleaved slice timing, smoothing in space with a Gaussian kernel of 6 mm FWHM, and high-pass filtering at 160 s. Participants with excessive head motion (>1 voxel translation or 2° of rotation) ($N = 2$) were excluded from further analysis. Functional images were normalized using each participant's high-resolution anatomical image (six degrees of freedom for registration to high-resolution image, twelve degrees for registration to standard space).

A general linear model (GLM) with twenty-two regressors of interest was fit in pre-whitened data space. A fixed-effects GLM was computed on an individual subjects level, and group-level analysis was computed using a mixed-effects model (FLAME). Six regressors were used to model the first 30 (F30), last 30 (L30), and mid 90 (M90) trials (excluding incorrect trials) separately for the blocks following the 12 s and 28 s breaks (post-short break, PS; post-long break, PL). A further six regressors modeled the events weighted by reaction times; these predictors were orthogonalized with their respective non-weighted regressors in order to account for the effects of RT on brain activation (Domagalik et al., 2014), and eliminate the influence of this confound. Two more regressors were added to model the effect of reaction time variability on brain activity in the PS and PL blocks for a similar reason (Esterman et al., 2013); these regressors were also orthogonalized with the earlier predictors in their respective blocks. Finally, eight additional nuisance regressors were included: one to model trials with incorrect responses, one to model the on-screen instructions, and six to account for the effects of head motion (3 translation, 3 rotation). All predictors that modeled task responses were 100 ms in length, and the predictor modeling instruction screens was 1 s in length. All regressors were convolved with a double-gamma hemodynamic response function. For the remainder of this report, we focus analysis on contrasts generated from the main effects of performing the BSDT (i.e., the first six regressors described above).

To test our study hypotheses, we separately combined F30, M90, and L30 events across PS and PL blocks and contrasted these against baseline (modeled implicitly) to observe the effect of time-on-task on activity associated with the BSDT. We did a further direct test of this by contrasting activation to the first and last 30 responses (F30 – L30; L30 – F30) in the PS and PL blocks combined. To measure the effects of taking breaks of differing lengths, we performed the following contrasts: F30-PS vs. F30-PL, L30-PS vs. L30-PL, and the interaction effect of break length and time-on-task. All contrasts were performed following the recommended procedures in FSL: they were specified at the first-level before being carried up to higher-level analysis.

A further subject-level mixed effects analysis was computed to assess the effects of individual differences in response to the break period. This model was identical to the one described above, but with the amount of recovery (mean % change in predicted RT) between PS and PL blocks entered as a between-subjects covariate.

All higher-level statistical analyses were performed with default FSL parameters, using cluster significance threshold $p = .05$ and Z threshold > 2.3. Peak percentage signal change was extracted using the featquery module within FSL.

Results

Behavioral findings

Overall accuracy (% correct responses) on the BSDT was high (mean = 97.3%, SD = 1.6%), indicating that participants were able to perform the symbol-character mapping. Across all subjects, median response time for each trial was 634 ms (SD = 127 ms).

We examined the overall trends of performance across the two task runs by subjecting median response time (RT) in the task blocks to 2-way repeated-measures ANOVA with BLOCK and RUN as factors (Fig. 2a). Box corrections were used due to violation of sphericity assumptions. We found a significant effect of BLOCK on RT ($F_{2.8,\ 72.8} = 7.83$, $p < 10^{-7}$), but no significant effect of RUN ($F_{1,26} = 0.91$, $p = .35$), and no RUN × BLOCK interaction ($F_{3.63,\ 94.3} = 1.47$, $p = .22$). These results indicate that long-term time-on-task trends persisted

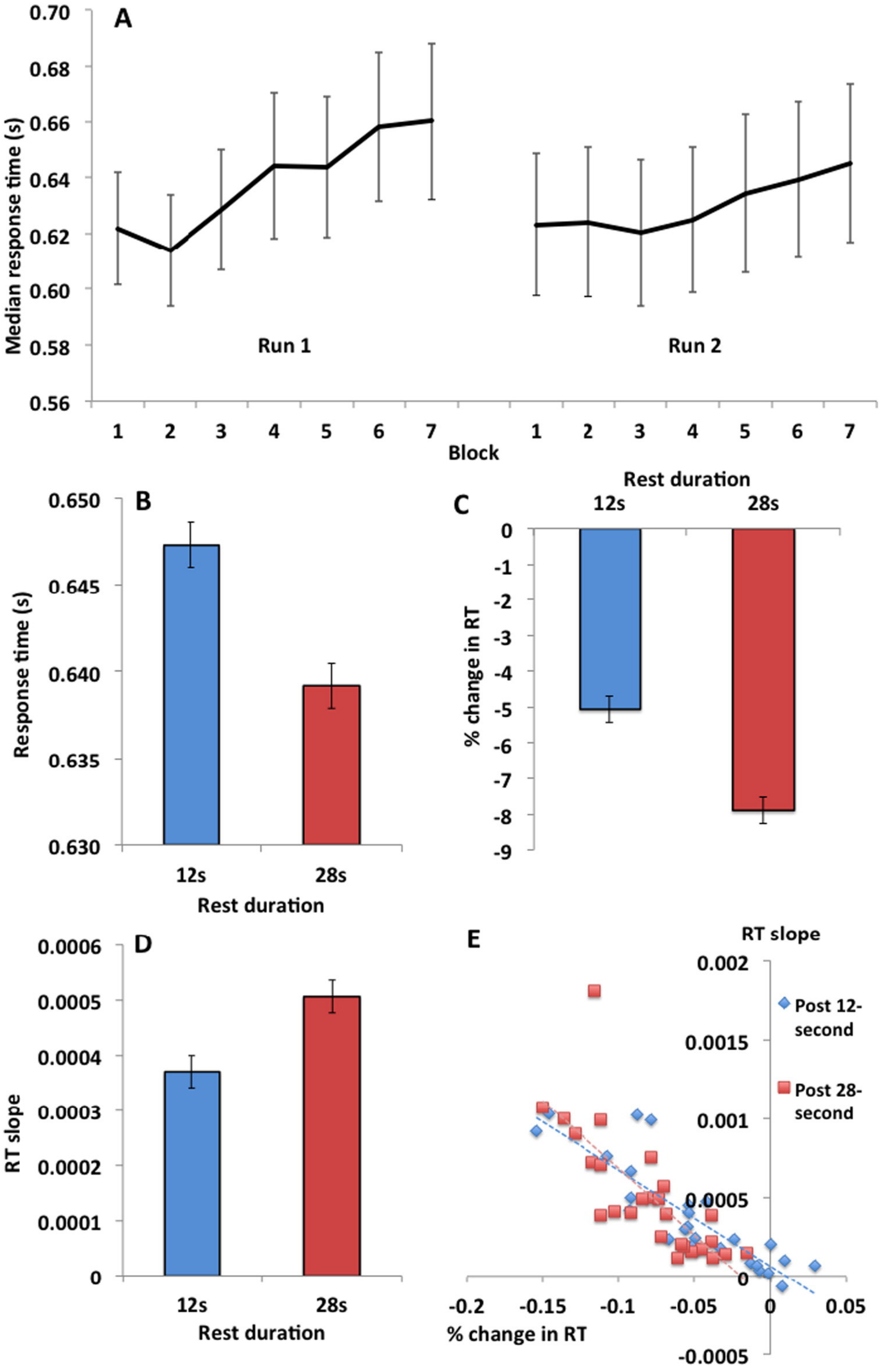

Fig. 2. Behavioral results. Error bars represent standard errors, and are corrected for within-subjects measurements in panels B–E. A) Response time increases significantly across task blocks within a run, but did not differ significantly between runs. B) Median RT was significantly shorter following 28 s than 12 s breaks. C) 28 s breaks led to significantly greater immediate reduction in RT. D) TOT slope in blocks following 28 s breaks were significantly steeper. E) For both the 12 s and 28 s breaks, immediate recovery was correlated with subsequent TOT decline.

across the task run, despite the breaks administered between blocks. However, the longer break (~6 min) in between task runs (during which the high-resolution anatomical scan was collected) was sufficient to restore performance such that there was no difference between runs. For simplicity, we thus combined data across runs for subsequent analysis.

To analyze the short-term trends of TOT within each task block, we computed linear fits to the RT data in each 150-trial block in order to estimate the slope of performance as well as the predicted RT at the beginning and end of each block. As a logarithmic or two-process fit may better describe the trend of time-on-task under certain circumstances (Giambra and Quilter, 1987; Lim et al., 2012), we also compared R^2

values between linear and logarithmic fits to the unsmoothed individual and group data. In both cases, R^2 for the linear fit was marginally greater than R^2 for the logarithmic fit (Individual: .078 vs. .074; Group: .549 vs. .539). Hence, we used slope and predicted RT values from the linear fits for further analysis.

We tested for the presence of time-on-task effects within each task block by comparing the estimated slopes (averaged by subject) in a one-tailed *t*-test against 0. This test was significant ($t_{26} = 6.92$, $p < 10^{-6}$; $d = 1.33$), suggesting that participants responded increasingly slowly over the course of the 150 trials in each block.

Turning to the effect of the rest breaks between blocks, we tested whether these intervals had a beneficial effect on performance overall by computing the change in predicted RT due to the break (i.e. % change of predicted RT at the end of a task block to the beginning of the subsequent block). On average, response times decreased (improved) by 37.17 ms (SD = 9.04 ms), or 6.48% (*SD* = 3.90%), and this improvement was significantly greater than 0 ($t_{26} = -9.12$, $p < 10^{-8}$; $d = 1.75$), indicating that participants performed the task faster on resumption after a rest break.

We next used paired *t*-tests to compare the magnitude of the improvement in RT between the short (12s) and long (28s) rest pauses, as well as the median RT and slope in the blocks following these different break lengths. We found significantly greater improvement after the long compared to the short break (5.1% vs. 7.9%; $t_{26} = 4.12$, $p = .0003$; $d = 0.79$), and that median RT was significantly faster in blocks following the long break (647 ms vs. 639 ms; $t_{26} = 3.26$, $p = .003$; $d = 0.63$) (Figs. 2b–c). However, we also found that the TOT slope was significantly steeper following the longer rest pause ($t_{26} = 2.39$, $p = .02$; d = 0.46) (Fig. 2d). Over both break lengths, the amount of recovery was negatively correlated with TOT slope (Fig. 2e: PS: $r = -.86$, $p < 10^{-9}$; PL: $r = -.69$, $p = .0008$). As these correlations may be confounded with speed at the start of the second block (and not just the improvement during the break), we ran partial correlations with the two variables above controlling for predicted RT at the start of block 2, and still found a significant association between them (PS: $r = -.85$, $p < 10^{-9}$; PL: $r = -.55$, $p = .003$). These findings closely mirror those we have reported in a previous experiment (Lim and Kwok, in press).

Neural correlates of within-block time-on-task

The main effect of performing the BSDT on brain activity was analyzed by contrasting all task blocks against baseline. As expected, we observed widespread activation in occipital regions, and left-lateralized activity in the frontoparietal attention network, as well as deactivation in the frontal pole and parts of the default-mode brain network (DMN) (Table 1). We then examined how this activity varied over the course of each task block by performing separate contrasts (against baseline) for the first 30 (F30), mid 90 (M90), and last 30 (L30) trials of each block. We adopted this conservative approach as our primary goal in this paper was to examine the periods directly before and after the breaks (see below), and to avoid making the assumption that BOLD activity increases linearly with time-on-task. When analyzed in this way, we observed steadily increasing activation in motor and executive control areas over the course of the run, with left-lateralized activity in F30 and increasingly bilateral activation over the course of the block (Fig. 3). We also observed steadily decreasing deactivation in the DMN from F30 to L30 (Fig. 4). A direct contrast of F30 and L30 (set at a higher threshold of $z > 5.0$, cluster corrected) showed significantly greater activation in left middle frontal gyrus (MFG), and bilateral precentral gyrus, among other regions (Table 2). Contrasting M90 with F30 and L30 with M90 yielded largely similar activation peaks; these results are omitted in the interest of space.

Table 1
Main effect of task performance. Clusters and peak voxels for the contrast showing activation during task performance, combining the first 30 (F30), last 30 (L30) and middle 30 (M30) events across all blocks.

	Cluster	Anatomical region	Number of voxels	MNI coordinates of local maxima X	Y	Z	Z-score
Activation	1	L superior parietal lobule	34 506	−30	−56	46	7.3
		L lateral occipital cortex		−28	−60	50	7.08
		L precentral gyrus/middle frontal gyrus		−36	−10	54	7.03
				−44	−12	50	7.01
		Cerebellum		18	−56	−26	7.01
				22	−56	−28	7
	2	L lateral occipital cortex	4140	−38	−88	−10	6.8
				−44	−66	−14	6.02
				−48	−80	−8	6
				−46	−68	−10	5.87
		Occipital pole		−30	−94	−14	5.82
				−32	−94	−8	6.33
Deactivation	1	R lateral occipital cortex	30 254	42	−78	38	6.83
				42	−80	28	6.23
				−8	−86	28	6.57
		Precuneus		4	−78	52	6.38
		Posterior cingulate gyrus		8	−40	44	6.22
		Occipital pole		12	−90	36	6.16
	2	Frontal pole	1243	−26	66	8	4.17
				−42	48	6	3.57
				−38	60	4	3.57
				−16	70	−18	3.16
				−26	60	26	3.12
				−38	48	28	3.1
	3		874	32	38	28	3.8
				26	68	−18	3.48
				28	72	−4	3.42
				26	62	−20	3.33
				28	74	4	3.27
				36	70	−14	3.09

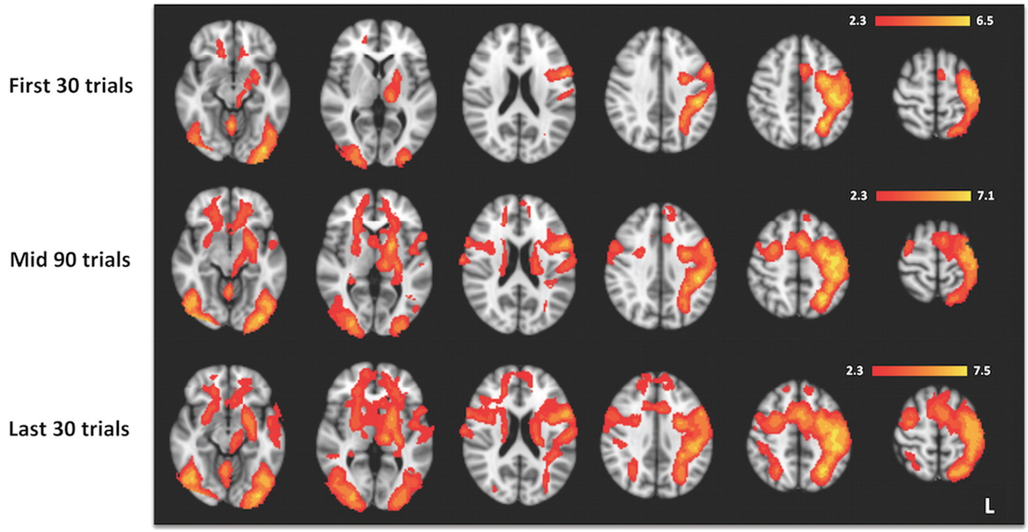

Fig. 3. Activation to the BSDT during the first 30, mid 90 and last 30 trials. Maps are thresholded at $p < .05$ (cluster-corrected).

Effects of break length on brain activity

We next tested the effect of the short and long breaks on fMRI activity during the first and last 30 trials of the block using 2-way ANOVA with planned contrasts F30-PS vs. F30-PL; L30-PS vs. L30-PL). There was significantly greater activity in the last 30 trials of the PS condition (i.e. after the short break) compared with the PL condition (i.e. after the long break) but not in the opposite contrast. Areas involved lay in the left MFG and left precentral gyrus, as well as in the cerebellum (Fig. 5). In line with these findings representing differential TOT effects, there was no significant difference in levels of activation when comparing the first 30 trials in the PS and PL conditions. There was also no significant interaction between break length and TOT.

To identify regions that could account for differences in the amount of recovery received in response to a break opportunity (Lim et al., 2013), we repeated the above analysis including the absolute difference in % RT improvement between PS and PL blocks as a between-subjects covariate. We found significantly greater activity when comparing the first 30 trials in the long vs. short break conditions in bilateral putamen extending downward into the right basal forebrain, amygdala, and parahippocampal cortex (MNI peaks: (28, 4. 0) and (−24, 12 −2)) (Fig. 6). When comparing the critical last 30 responses across the PS and PL conditions, we again observed activation in a more circumscribed area in the left MFG (MNI peak: (−26, 0, 48)), as well as the cerebellum (Fig. 6). For illustrative purposes, parameter estimates extracted from this area are plotted against individual differences in % RT improvement. From these plots, we can see that the greater the amount of recovery a participant received in the long compared to the short break, the greater their activation in the putamen during the first 30 trials in the PL condition, and the greater their activation in left MFG during the last 30 trials in the PL condition.

Discussion

In the present work, we found that the length of mid-task rest breaks in a self-paced task changes the implicit allocation of effort or resource deployment in the post-break period. These findings resemble those of a recent study involving a lengthy, work-paced task (Lim and Kwok, in press) and extend those findings to a context where work and rest

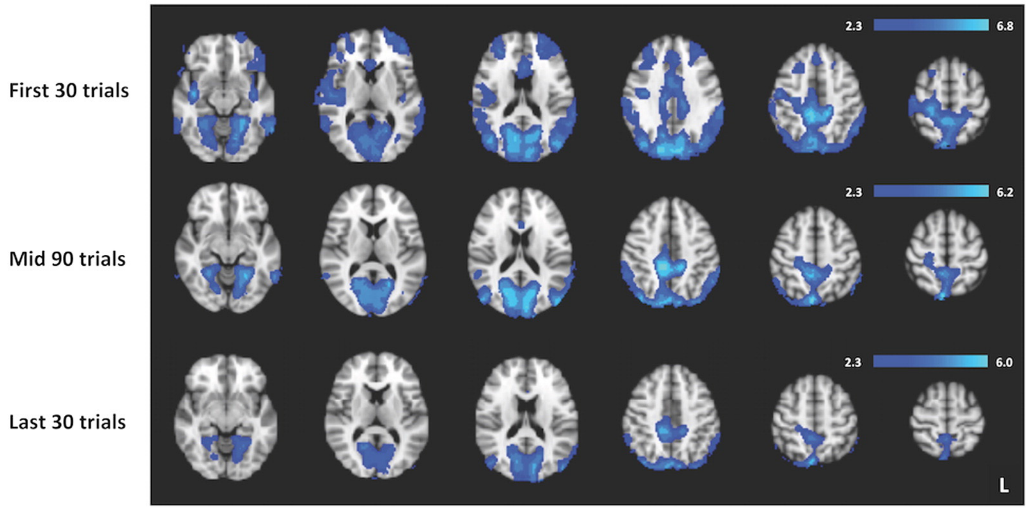

Fig. 4. Deactivation to the BSDT during the first 30, mid 90 and last 30 trials. Maps are thresholded at $p < .05$ (cluster-corrected).

Table 2
Activated regions in the L30–F30 contrast. Clusters and peak voxels for the contrast of the last 30 (L30) against the first thirty (F30) events across all blocks. No voxels were significantly activated in the F30 > L30 contrast. For brevity, clusters with fewer than 100 voxels are not reported if their peaks lie in the same anatomical region as a larger cluster.

Cluster	Anatomical region	Number of voxels	MNI coordinates of local maxima			Z-score
			X	Y	Z	
1	L precentral gyrus	4827	−44	−6	50	6.83
			−52	−6	40	6.82
			−48	−6	44	6.5
	Paracingulate gyrus		10	12	52	6.58
	L middle frontal gyrus		−26	2	54	6.57
			−28	8	46	6.45
2	L lateral occipital cortex	1699	−44	−80	−12	6.29
			−24	−80	26	6.17
			−34	−78	−4	5.84
			−38	−78	−18	5.79
	L fusiform gyrus		−32	−72	−18	5.92
	L superior parietal lobule		−20	−56	56	5.91
3	R precentral gyrus	1081	50	−12	48	6.49
			46	−8	48	6.27
	R postcentral gyrus		50	−18	52	6.45
			64	−8	22	6.17
			42	−26	58	6.11
			54	−8	34	5.82
4	R lateral occipital cortex	615	28	−82	26	5.83
			18	−84	32	5.61
			42	−80	0	5.59
			34	−84	14	5.54
			28	−86	16	5.44
			26	−88	10	5.25
5	Frontal pole	179	−32	44	12	5.8
			−28	54	6	5.6
			−26	52	0	5.55
			−28	52	−6	5.52
			−38	44	12	5.31
			−26	40	14	5.09
6	R lateral occipital cortex	123	18	−58	58	5.65
	R precuneus		10	−60	58	5.41
7	R planum temporale	44	58	−22	10	5.38
			60	−22	14	5.33
8	R lingual gyrus	36	12	−78	−12	5.36
			14	−84	−12	5.28
9	L thalamus	22	−16	−4	10	5.62
10	L middle temporal gyus	26	−64	−48	2	5.63
11	R supramarginal gyrus	13	−58	−26	24	5.47

blocks are of a short duration. Faster responding in the immediate aftermath of a long break was associated with greater activation in the putamen. However, by the end of the block, participants with larger recovery from the break had shown a steeper decline in performance, as well as higher levels of activation in left MFG, suggesting that degraded performance occurs despite the increasing exercise of cognitive control.

Identical behavioral patterns despite different task characteristics

Across the work-paced and self-paced tasks we have studied, we observe a common pattern of responding when mid-task breaks of different lengths are administered. On average, rest breaks interrupt TOT-related declines, and improve performance, both in laboratory and real-world tasks (Tucker, 2003; Ross et al., 2014; Helton and Russell, 2015). Moreover, as break length increases, participants tend to show greater immediate improvement in response times. However, TOT decrements also tend to be steeper following long versus short breaks, with a negative correlation between these decrements and the benefit received due to the break (Lim and Kwok, in press). As patterns of TOT decline differ between work- and self-paced tasks (Broadbent, 1953; Steinborn et al., 2010), it is notable that we find the same correlation across both these kinds of paradigms.

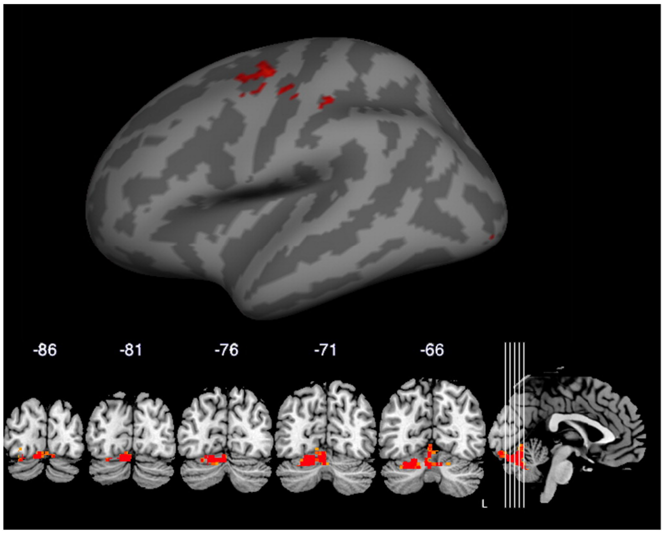

Fig. 5. Brain regions with greater activation for L30-PL > F30-PL. The left middle frontal gyrus and cerebellum are more active at the end (last 30 trials) of blocks following longer breaks.

We previously interpreted this phenomenon in the context of resource recovery and effort allocation (Lim and Kwok, in press), borrowing ideas from the resource-control model of sustained attention proposed by Thomson et al. (2015). In this model, increasing TOT leads to reductions in executive control, which makes on-task activity increasingly difficult to sustain. This reduction in executive control comes about because the default state of the brain is mind wandering, and inhibiting mind-wandering uses up executive resources that are needed to effectively perform the primary task. As a corollary to this, allowing more time for the effects of TOT to dissipate during a rest period, putatively by allowing the brain to engage in a period of non-focused activity that does not require executive control, should correspondingly lead to greater restoration of the resources needed to effectively sustain on-task activity after the break.

The resource-control model improves upon pure resource-depletion accounts in explaining time-on-task phenomena (Thomson et al., 2015). Nevertheless, it still seems inadequate in accounting for the differences in time-on-task slopes observed following breaks of differing lengths, and only partially explains the patterns we observe in our fMRI data. A more nuanced version of the resource-control model that is supported by the current data might take into account time-varying roles of both the bottom-up (automatic) and top-down (executive) modules that underlie sustained attention (Schneider and Chein, 2003; Sarter et al., 2006). Specifically, faster responding at the beginning of the task block following long breaks may relate to greater automaticity, while slower responding by the end of these blocks is seen in tandem with greater engagement of controlled processing. We note that these effects are likely to be task-dependent; automaticity may hinder good performance in (say) paradigms that require inhibition of prepotent responses. Our fMRI data, discussed below, support this formulation.

Recruitment of fronto-parietal areas increases with time-on-task

Several previous studies on mental fatigue have implicated the frontoparietal executive network in TOT-related performance declines. Early PET studies by Paus et al. (1997) and Coull et al. (1998), as well as a study by Lim et al. (2010) using arterial spin labeled fMRI showed decreases in CBF in executive control regions paralleled by worsening performance. Decreases in activation with TOT accompanied by performance decline have also been shown using BOLD fMRI (Asplund and Chee, 2013).

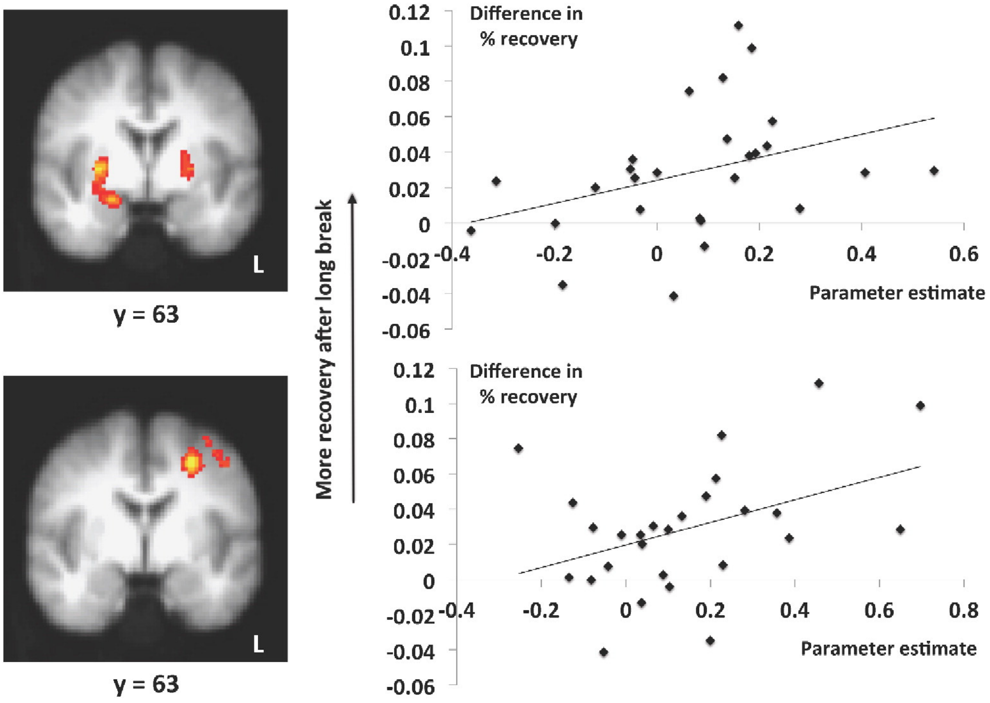

Fig. 6. Covariate analysis. % difference in change in predicted RT over the 12 s and 28 s breaks was entered as a between-subjects covariate. In this new model, we observed Top: Activation in the putamen in the contrast between the first 30 trials following the 28 s vs. the 12 s break. Bottom: Activation in left middle frontal gyrus in the last 30 trials following the 28 s vs. the 12 s break. Correlations between parameter estimates from the ROI are displayed to illustrate the direction of these effects.

More recent work has employed whole-brain functional connectivity analysis to interrogate the effects of mental fatigue. These studies have shown that TOT leads to changes in brain topology (i.e. clustering and path length) that result in reduced efficiency of information transfer within the cortex (Breckel et al., 2013; Giessing et al., 2013; Sun et al., 2014a, 2014b). Sun et al. (2014a) additionally showed that fatigue-related connectivity changes are asymmetric across hemispheres, with significant decreases in left, but not right frontoparietal connectivity on a test of sustained attention.

Unlike the studies cited above, our current paradigm unexpectedly revealed greater engagement of frontoparietal areas with increasing TOT. As we explicitly included RT- and RT-variability-weighted regressors in our model, this difference cannot simply be attributed to the longer RTs observed at the end compared to the start of task blocks. As this pattern of increasing rather than decreasing activation is at odds with a prior study (Asplund and Chee, 2013), we recalled a subsample ($N = 18$) of participants and scanned them as they underwent the identical paradigm (a rapid serial visual presentation task) to that performed previously. We essentially replicated these findings (Supplementary Figure 2), observing decreases in activation over task blocks and in task-positive areas.

The most likely explanation for this discrepancy is due to task differences between this and prior work. Previous experiments have all employed paradigms involving target monitoring (e.g. the Psychomotor Vigilance Test (Lim and Dinges, 2010), and the rapid serial visual presentation task shown in Supplementary Figure 2). In contrast, the BSDT demands awareness of multiple stimulus-to-response mappings, in addition to timely motor responses. Hence, we suggest that TOT may only lead to decreases in activation over time in paradigms in simple tasks where a binary decision is required (e.g. target vs. non-target) (Manly et al., 1999). In tasks requiring more complex processes as well as the constant engagement of controlled attention, increases in frontoparietal activity over time may instead be seen. Other factors (e.g. efficiency of resource deployment) may also account for these differences. Nevertheless, we suggest that the same underlying principles apply to all these data: that the brain trades off between these two systems depending on factors such as time-on-task and task demands.

Deactivation in default-mode areas decreases with time-on-task

In contrast with the task-positive network, we observed steadily declining levels of deactivation in the DMN from F30 to M90 to L30. Failure to suppress activity in this network is typically associated with disengagement from online task performance (Weissman et al., 2006) and activation of the network is associated with mind-wandering (Christoff et al., 2009). Furthermore, stronger anti-correlations between DMN and fronto-parietal networks are associated with superior task performance (Kelly et al., 2008). Low frequency fluctuations in resting-state periods prior to task performance have also been reported to predict TOT declines (Gui et al., 2015). Although we did not measure this specifically, we speculate that reduced DMN deactivation in the current dataset may be associated with the reduced direction of attention to the external environment. This finding is congruent with other experiments showing that mind-wandering typically increases with time-on-task (Smallwood and Schooler, 2006).

Differential engagement of putamen and MFG following breaks of different lengths

Using the difference in the amount of recovery received in the long versus the short break as a between-subjects covariate, we found greater activation in the putamen and basal forebrain in the first trials of the block following a long break, and greater activation in the left MFG in the last trials of such blocks.

Although the putamen has been implicated generally with motor performance and motor tasks (Alexander et al., 1986), its role in these is non-specific (Vink et al., 2005). It has been demonstrated that the putamen plays a role in motor learning (Poldrack et al., 2005; Hardwick et al., 2013), such that the sensorimotor territory of the putamen shows higher activation post learning. This suggests that the putamen is involved with the automatic generation of motor responses, a theory further corroborated by Lehéricy et al. (2005), who showed activation changes within this area from learning through to automaticity. As participants were given ample opportunity to learn the task paradigm, our results showing the correlation of putamen activity with greater performance recovery are unsurprising.

However, the results from our covariate analysis also indicate that the superior performance observed in the F30-PL period is not cost-free, but that greater executive control is later required to putatively make up for this high level of early performance. The MFG is well established as a region associated with top-down attentional control (Hopfinger et al., 2000; Corbetta and Shulman, 2002; Fan et al., 2005), and its correlation with performance at the end of the task block suggests its increasing involvement as the need for compensatory effort increases. This finding is in agreement with Demeter et al. (2011) who manipulated the amount of distraction in a test of sustained attention, leading to overall increases in right MFG activation. Using individual differences analysis, these researchers also found that greater increases in this frontal activation were correlated with greater behavioral vulnerability.

Greater cerebellar activity was also observed at the end of PL compared to PS blocks. The cerebellum is active during sustained attention tasks (Lawrence et al., 2003), and particularly when motor preparation is required (Langner and Eickhoff, 2013). Thus, differences in the effort required for motor preparation on the BSDT may also ensue as a result of the differing TOT profiles following long and short breaks.

In sum, we report a potential neural mechanism underlying a novel behavioral pattern observed following task breaks of differing lengths, which suggests a shift in the balance between top-down and bottom-up attentional control. Taking a longer break prompts participants to engage more automatic processing in the immediate aftermath of the break, and more controlled processing by the end of the corresponding task block. Further studies are needed to uncover the underlying reasons for these strategy shifts, and why higher levels of initial automatic responding come at a later cost.

Practical implications

As many white-collar jobs in the modern workplace are self-paced, our current findings represent a step towards more ecologically valid theories of sustained attention and TOT. They may hold particular importance for jobs in which consistent performance over time is important. For example, a study by Basner et al. (2008) suggests that luggage screening agents might be highly prone to TOT effects and sleep loss, affecting their ability to detect target contraband objects in a complex array. The tradeoff between stability and speed that is mediated by rest could be a crucial consideration in these and similar work settings. The neural findings from the current work reinforce that this tradeoff is due to differences in both automatic and top-down modules, and caution against focusing exclusively on top-down failure as the mechanism of TOT decline. Our results may also explain the results of older field studies showing that regular short breaks result in more stable task performance, and fewer errors (Kopardekar and Mital, 1994; Dababneh et al., 2001). However, further research on the generalizability of our findings to real-world tasks and longer time scales is necessary before prescriptions for work–rest schedules can be made.

Conclusion

In summary, the results of this study provide additional evidence that varying the time allowed for recovery also directs participants to implicitly alter the way they allocate resources in the subsequent work period. Future research may address if this is the case for even more complex real-world tasks, as is hinted at by the time-limited recovery afforded by breaks in these contexts (Tucker et al., 2003), as well as how best to arrange rest and work periods to accommodate this new knowledge.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2016.03.077.

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