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In the Zone or Zoning Out? Tracking Behavioral and Neural Fluctuations During Sustained Attention

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Despite growing recognition that attention fluctuates from moment-to-moment during sustained performance, prevailing analysis strategies involve averaging data across multiple trials or time points, treating these fluctuations as noise. Here, using alternative approaches, we clarify the relationship between ongoing brain activity and performance fluctuations during sustained attention. We introduce a novel task (the gradual onset continuous performance task), along with innovative analysis procedures that probe the relationships between reaction time (RT) variability, attention lapses, and intrinsic brain activity. Our results highlight 2 attentional states—a stable, less error-prone state ("in the zone"), characterized by higher default mode network (DMN) activity but during which subjects are at risk of erring if DMN activity rises beyond intermediate levels, and a more effortful mode of processing ("out of the zone"), that is less optimal for sustained performance and relies on activity in dorsal attention network (DAN) regions. These findings motivate a new view of DMN and DAN functioning capable of integrating seemingly disparate reports of their role in goal-directed behavior. Further, they hold potential to reconcile conflicting theories of sustained attention, and represent an important step forward in linking intrinsic brain activity to behavioral phenomena.

Keywords: continuous performance task, default mode network, dorsal attention network, fMRI, vigilance

Introduction

Sustaining a moderate level of attention over time is critical to performance of many everyday activities, such as driving, reading, or listening to a lecture. Remaining focused is challenging however and, in reality, our attention waxes and wanes. At times, our attention is focused on our task goals, while at others our focus is lost through distraction, fatigue, or lack of motivation. Although such fluctuations in attention are commonplace, and may even be characteristic of sustained performance, only recently has research been dedicated to better understanding their relationship to ongoing brain activity.

The ability to maintain attention for prolonged durations was first studied during World War II to understand why radar operators failed to detect targets later in their shifts (Mackworth 1948). Human factors psychologists developed a number of tasks to study how sustained attention fails over time, known as the vigilance decrement. These investigations demonstrated that sustained attention is effortful (Warm et al. 2008), and that vigilance decrements can lead to accidents in real world situations (Molloy and Parasuraman 1996). This line of research has largely supported a model that views sustained attention failures as the result of resource depletion, or "overload," whereby attentional resources are drained by continued performance (Davies and Parasuraman 1982; Helton and Warm 2008; Warm et al. 2008). These classic methods are not ideal for studying moment-to-moment attention fluctuations however, as they sample behavior infrequently, with rare targets separated by extended periods of response-free "vigil" or "watchfulness." In addition, they tend to be time consuming, eliciting vigilance decrements over many minutes or even hours, which is clearly not optimal for most types of functional neuroimaging.

More recently, other types of continuous performance tasks (CPTs) that have the advantage of sampling behavior more frequently have been used to study sustained attention. In these variants of CPTs (e.g. the sustained attention to response task [SART]; Robertson et al. 1997; Conners' CPT-II; Conners 2000), participants are required to respond on most trials, with rare "stop" trials serving as targets. Lapses in sustained attention thus manifest as errors of commission (i.e. failing to withhold response). In contrast to "overload" theories, this line of research has promoted a model of sustained attention in which underarousal or boredom (i.e. "underload") contributes to lapses in performance. In support of this account, self-report methods have demonstrated that mind-wandering, or task-unrelated thought, tends to precede such lapses (Smallwood and Schooler 2006), suggesting that they occur when attention is momentarily directed away from task performance, as task performance becomes more automated. While SART-like CPTs are thus more sensitive to momentary changes in attentional state than classic vigilance tasks, they often fail to elicit performance decrements in healthy individuals, calling into question whether they sufficiently tax sustained attention. Instead, trials in these tasks are accompanied by abrupt visual onsets, which may exogenously capture attention (Yantis and Jonides 1984), serve as alerting cues (Sturm and Willmes 2001), and reduce demands on endogenous maintenance of attention. Consistent with this idea, sudden-onset visual cues presented before target stimuli have been shown to attenuate declines in perceptual sensitivity in a vigilance task (MacLean et al. 2009). In addition, the brief fixation intervals that fall between trials on SART-like CPTs may provide short breaks, preempting performance declines.

Though fluctuations in sustained attention are commonly assessed with accuracy measures, another way in which subtler trial-to-trial variations have been explored is through the analysis of reaction time (RT) variability, or intraindividual variability (IIV). IIV is sensitive to the cognitive changes accompanying a wide range of psychiatric and neurological disorders, as well as normal development and aging (see

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MacDonald et al. 2006, 2009) and has been specifically linked to impairments of attention and executive function (West et al. 2002; Stuss et al. 2003; Sonuga-Barke and Castellanos 2007). For example, individuals with attention deficit hyperactivity disorder (ADHD) exhibit significantly more variable correct RTs, even when controlling for overall speed (for review see Castellanos et al. 2006), marked by exacerbation of attentional fluctuations occurring roughly every 12–40 s (Vaurio et al. 2009). Critically, analyses of IIV have generally been limited to differences across groups or task conditions, and have yet to explore within-subject response variability as attention declines over time, or presumably fluctuates between different states of task engagement (although see Faulkner 1962).

Current understanding of the neural systems supporting attention derives largely from studies that experimentally manipulate acts of goal-directed attention. These studies have underscored the importance of 2 large-scale brain networks: the dorsal frontoparietal attention network (DAN) and the default mode network (DMN). In general, the DAN is engaged by goal-directed attention, and damage to this system can lead to attentional and executive dysfunction. In contrast, the DMN, which includes ventral and medial aspects of frontal and parietal cortex, is deactivated during acts of attentional control, showing greater activity during rest than during task performance. More recently, these networks have also been implicated in intrinsic, trial-by-trial variations in performance, though disagreements exist as to the nature of their contributions. Whereas some studies have suggested that greater ongoing activity in DAN regions is predictive of more efficient performance (e.g. reduced error likelihood, Padilla et al. 2006; Boly et al. 2007; O'Connell et al. 2009; enhanced cognitive flexibility, Leber et al. 2008; reduced distractibility, Leber 2010; faster responding, Weissman et al. 2006), others have found greater baseline activity in DAN regions associated with poorer performance (e.g. poorer target detection, Sadaghiani et al. 2009). Similarly, high levels of ongoing activity in DMN regions have been linked to mind-wandering (Christoff et al. 2009) and less efficient performance (e.g. greater error likelihood, Boly et al. 2007; Li et al. 2007; Eichele et al. 2008; slower responding, Weissman et al. 2006), but have also been associated with faster responding (Gilbert et al. 2006; Hahn et al. 2007), better target detection (Sadaghiani et al. 2009), and more practiced, effortless performance (Mason et al. 2007). Thus, there is little consensus as to whether high ongoing DAN or DMN activity is beneficial or detrimental, leaving open the possibility that such absolute statements may not be possible. Instead, it may be that optimal performance relies on intermediate levels of activity or emerges from a balance between the 2 networks, such that looking at either one in isolation could prove misleading.

The current study aimed to clarify the behavioral and neural correlates of moment-to-moment fluctuations in sustained attention, with a particular focus on the roles of the DAN and DMN. We designed a novel task, the gradual onset CPT (gradCPT), to reduce the abrupt, trial-based nature of traditional CPTs (See Fig. 1*A* and Supplementary Movie 1). We observed vigilance decrements over the course of the task, indicating that the gradCPT successfully taxed participants' ability to sustain attention. Further, using an innovative analysis procedure, we observed within-subject fluctuations in RT stability, which revealed 2 attentional states- a stable, less error prone state, or "in the zone," and an erratic, more error prone state, or "out of the zone." When "in the zone",

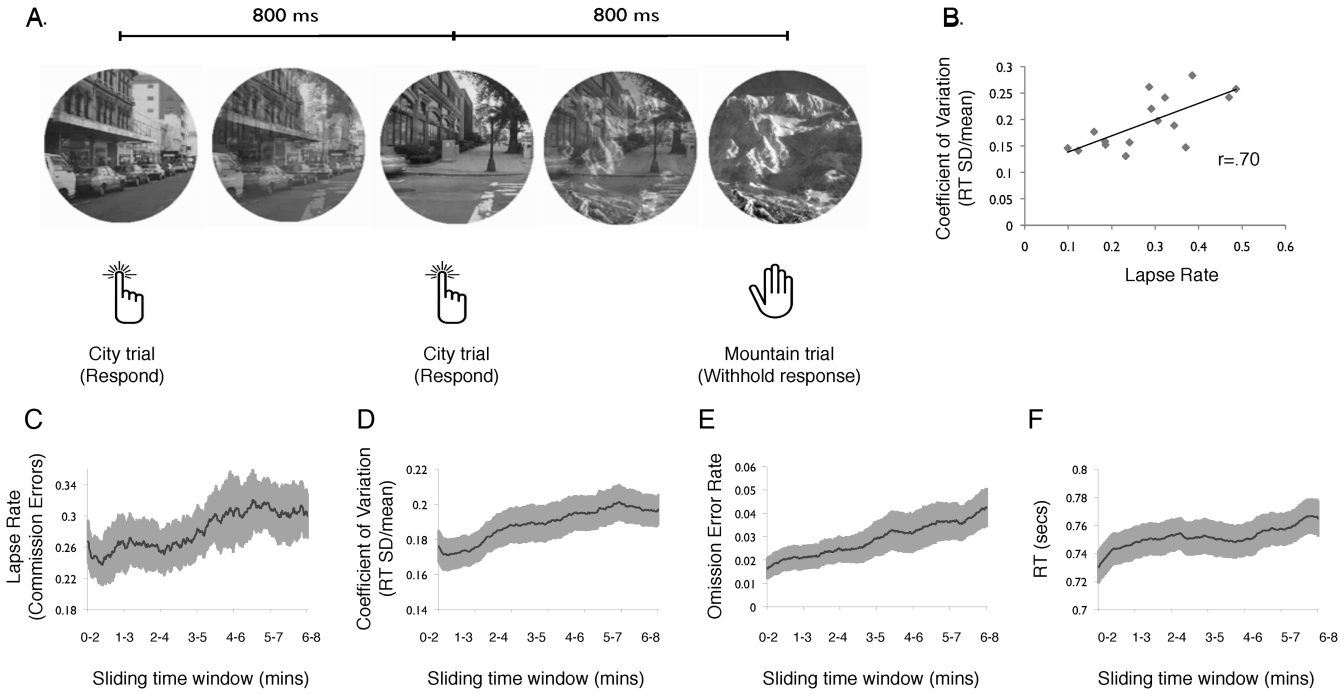

Figure 1. The gradCPT. (*A*) Illustration of gradCPT. Scenes gradually transition from one to the next each 800 ms. Participants are instructed to respond to city scenes and withhold for mountain scenes. (*B*) Participants who made more lapses (commission errors) responded more variably on baseline (correct commissions; responding to city scenes) trials (RT coefficient of variation; SD/mean; $r = 0.701$, $P < 0.01$). (*C*) Participants gradually made more lapses (commission errors; responding to mountain scenes) across each 8-min run (slope > 0, $P < 0.01$). (*D*) Participants' correct response times became more variable across each 8-min run (slope > 0, $P < 0.001$). (*E*) Participants gradually made more omission errors (failing to respond to city scenes) across each 8-min run (slope > 0, $P < 0.05$). (*F*) Participants' correct response times became slower across each 8-min run (slope > 0, $P < 0.05$).

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extreme peaks in DMN activity were predictive of subsequent errors. In contrast, when "out of the zone", reduced activity in DAN and task-relevant sensory regions (parahippocampal place area; PPA) was predictive of subsequent errors. Overall, however, RT stability was positively correlated with activity in the DMN, such that moderate DMN activity benefited performance. Taken together, these results motivate a more nuanced account of the potential influences of "overload" and "underload" on attentional performance, and encourage a broader view of the functions of the DMN and DAN.

Materials and Methods

Participants

Sixteen participants (6 males, ages 18–34 years, mean age = 24.1 years) performed the gradCPT during functional magnetic resonance imaging (fMRI) data collection. All participants were right handed, with normal or corrected-to-normal vision and no reported history of major medical illness, head trauma, neurological, or psychiatric disorder. The study was approved by the VA Boston Healthcare System IRB, and written consent was obtained from all participants.

Paradigm and Stimuli

The gradCPT contained 10 round, grayscale photographs of mountain scenes and 10 of city scenes. These scenes were randomly presented with 10% mountain and 90% city, without allowing the identical scene to repeat on consecutive trials. Scene images gradually transitioned from one to the next, using a linear pixel-by-pixel interpolation, with each transition occurring in 800 ms. Images were projected to participants through a MR compatible goggle system (VisuaStim Digital, Resonance Technology Inc.), and subtended a radius of 2.2° of visual angle. Participants were instructed to press a button for each city scene, and withhold responses to mountain scenes (See Fig. 1*A* and Supplementary Movie 1). Response accuracy was emphasized without reference to speed. However, given that the next stimulus would replace the current stimulus in 800 ms, a response deadline was implicit in the task.

Localizer Tasks

Two additional functional runs were conducted in order to independently localize 1) the DMN; 2) the DAN; and 3) scene-selective regions in the parahippocampal cortex (PPA). To identify the DMN and DAN, a 6-min resting scan was collected and submitted to independent component analysis (ICA) (details below). To identify PPA, a task was administered that was matched to the gradCPT in terms of timing, stimulus size, and low-level visual characteristics, in which scenes and faces alternated every 30 s and rare targets were identified by button press. Scene and face blocks were contrasted to identify PPA.

Procedure

Before scanning, participants were first familiarized with each of the 20 scene images (labeled as "city" or "mountain"), followed by a 1–2 min practice of the main task. In the MRI scanner, participants performed three 8-min runs of the gradCPT, a single 6-min run of the PPA localizer, and 1 run of a blocked gradCPT (data not presented). In addition, a 6-min eyes-closed resting scan was conducted for 13 of 16 subjects. An anatomical magnetization prepared rapid gradient echo (MPRAGE) was also acquired. The 3 gradCPT runs began the scan session, with the anatomical or resting scan introduced as a break between either run 1 and run 2 or run 2 and run 3. This break was included to reduce any cumulative load from 1 run to the next. The remainder of the session included the anatomical/resting scan, the blocked gradCPT run, and lastly the PPA localizer.

Imaging Parameters

Scanning was performed on a 3T Siemens MAGNETOM Trio system equipped with a 12-channel head coil, at the VA Boston Neuroimaging Research Center. Functional runs included 248 (gradCPT) or 188 (PPA localizer and resting scan) whole-brain volumes acquired using an echo-planar imaging sequence with the following parameters: repetition time (TR) = 2000 ms, echo time (TE) = 30 ms, flip angle = 90°, acquisition matrix = 64 × 64, in-plane resolution = 3.0 mm^2, 33 oblique slices, slice thickness = 3, 0.75 mm gap. MPRAGE parameters were as follows: TE = 3.32, TR = 2530 ms, flip angle = 7°, acquisition matrix = 256 × 256, in-plane resolution = 1.0 mm^2, 176 sagittal slices, slice thickness = 1.0 mm.

Behavioral Analyses

Reaction Time

RTs were calculated relative to the beginning of each image transition, such that an RT of 800 ms indicates a button press at the moment image n was 100% coherent and not mixed with other images. A shorter RT indicates that the current scene was still in the process of transitioning from the previous, and a longer RT indicates that the current scene was in the process of transitioning to the subsequent scene. So, for example, an RT of 720 ms would be at the moment of 90% image n and 10% image $n-1$, and so forth. On rare trials with highly deviant RTs (before 70% coherence of image n and after 40% coherence of image $n+1$) or multiple button presses, an iterative algorithm maximized correct responses as follows. The algorithm first assigned unambiguous correct responses, leaving few ambiguous button presses (presses before 70% coherence of the current scene and after 40% coherence of the following scene or multiple presses occurred on <5% of trials). Second, ambiguous presses were assigned to an adjacent trial if 1 of the 2 had no response. If both adjacent trials had no response, the press was assigned to the closest trial, unless one was a no-go target, in which case subjects were given the benefit of the doubt that they correctly omitted. Finally, if there were multiple presses that could be assigned to any 1 trial, the fastest response was selected. Slight variations to this algorithm yielded highly similar results, as most button presses showed a 1–1 correspondence with presented images.

Accuracy

Trials in which participants correctly inhibited a button press to mountain scenes were considered correct omissions. Trials in which participants erroneously responded to mountains were considered commission errors. Errors of omission, or failing to respond to city scenes, occurred rarely (average of 3% across participants). Omission errors were thus not considered in the fMRI analyses, although we report these behaviorally for completeness. The majority of trials, in which participants responded correctly to city scenes, were considered correct commissions. Commission error trials are subsequently referred to as "lapses," correct omissions as "correct" trials, and correct commissions as "baseline" trials.

Vigilance

Vigilance decrements were calculated with a 2-min sliding window around performance measures of interest [mean RT, RT variance (coefficient of variation = standard deviation of RT/mean RT), and accuracy], where the first window included 0–2 min and the last included 6–8 min. The window moved in increments of 1 trial, such that an estimate of each variable was calculated at each trial, with the exception that the first window centered on the trial at 1 min (0–2 min window), and the final window around minute 7 (6–8 min window). A 2-min window size was selected such that reliable estimates of lapse rate were possible, as an average 15 no-go trials occurred in each window. A linear slope (computed as rate of change per minute) was then calculated for each run and averaged across runs for each subject. One-sample *t*-tests were conducted to determine if these slopes differed from zero.

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RT Variability

Beyond mean RT and error rates, we were particularly interested in trial-to-trial variation in RT, which we assessed via a novel within-subject analysis that we called the variance time course (VTC). VTCs were computed from the ~500 correct responses in each run (following z-transformation of RTs within-subject to normalize the scale of the VTC), where the value assigned to each trial represented the absolute deviation of the trial's RT from the mean RT of the run (see Fig. 2*A*). We reasoned that deviant RTs, whether fast or slow, represented reduced attention to the task as follows: extremely fast RTs often indicate premature responding and inattention to the potential need for response inhibition (Cheyne et al. 2009; also confirmed by the results presented in Figure 2*B*, which demonstrate that lapses are preceded by response speeding), while extremely slow RTs might indicate reduced attention to or inefficient processing of the ongoing stream of visual stimuli, requiring more time to accurately discriminate scenes (Weissman et al. 2006). Values for trials without responses (omission errors and correct trials) were interpolated linearly, such that the missing value(s) were linearly estimated from RTs of the 2 surrounding trials. A smoothed VTC was computed using a Gaussian kernel of 9 trials (~7 s) full-width at half-maximum (FWHM), thus integrating information from the surrounding 20 trials, or 16 s, via a weighted average. This choice was based on prior work linking fluctuations around this frequency to attentional impairments (Di Martino et al. 2008). Though there are potentially several ways to assess the within-subject relationship between variability and accuracy (both behaviorally and neurally), we chose to divide performance into low- or high-variability epochs (later referred to as "in the zone" and "out of the zone") with a median split on the smoothed VTC for each run. This yielded 4 min each of being "in the zone" and "out of the zone". We chose this dichotomous approach, as it was conservative and straightforward, and defined each subjects' states relative to their own overall performance.

fMRI Analysis

General Methods

fMRI data was processed using Analysis of Functional NeuroImages (AFNI; Cox and Hyde 1997) and custom routines written in Matlab (Mathworks). Preprocessing steps included slice-time correction, motion correction using a 6-parameter, rigid body, least-squares alignment procedure, spatial smoothing to an 8-mm FWHM Gaussian kernel, automated coregistration and normalization of anatomical and functional volumes to Talairach space, and scaling of functional dataset values to percent signal change. Data from individual participants were analyzed with linear multiple regression (details below). Regression coefficients for effects of interest were compiled across participants and evaluated via voxelwise group-level *t*-tests. All resulting statistical maps were corrected for multiple comparisons using voxel-cluster Monte-Carlo-type α simulations (Forman et al. 1995), resulting in a corrected significance level of $\alpha = 0.05$ (individual-voxel intensity threshold of $P < 0.01$, cluster size of 54 contiguous voxels).

Identifying Functional Networks and Regions of Interest

Data from the blocked design PPA localizer were analyzed via convolution of boxcar task functions with an incomplete gamma function. To define right and left PPA, spherical ROIs (6-mm radius) were

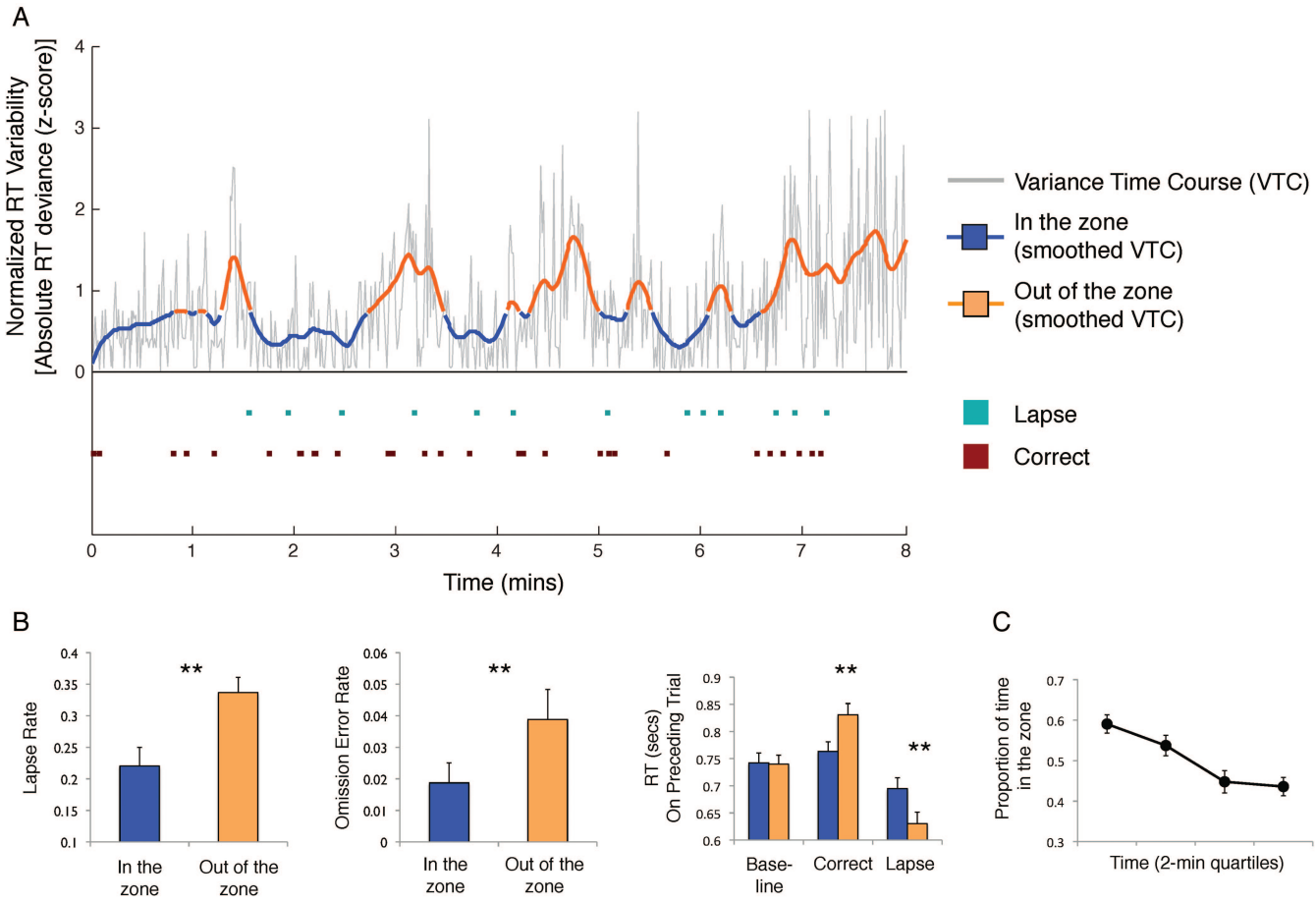

Figure 2. Reaction time stability as a measure of attentional state. (*A*) An example of a VTC for 1 run in a representative subject. (*B*) Participants made more lapses (commission errors) and omission errors when "out of the zone", than when "in the zone" (left and middle). Participants had larger speed-accuracy trade-offs when "out of the zone", such that faster RTs preceded lapses, and slower RTs preceded correct trials (correct omissions). Mean RT for baseline trials (correct commissions) did not differ between periods of being in or "out of the zone" ($P > 0.4$). (*C*) Proportion of time spent "in the zone" by quartile (2 min).**$P < 0.01$.

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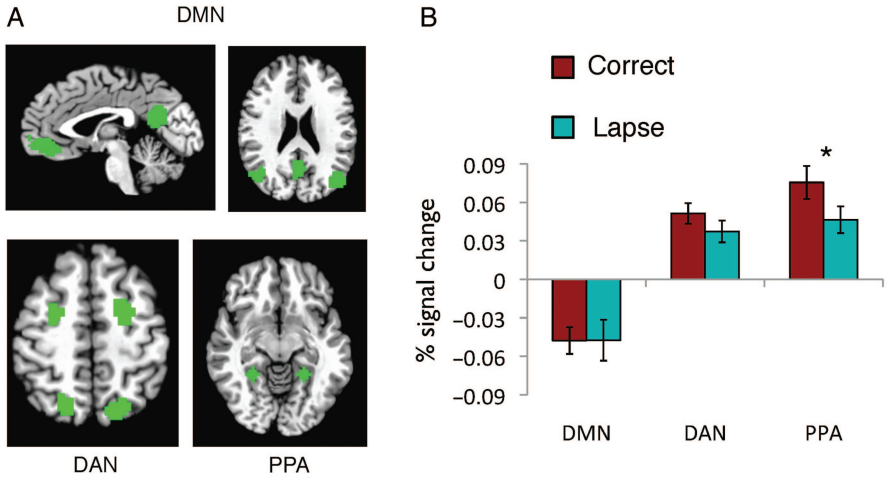

Figure 3. Functional networks and evoked BOLD response to mountain/target events (average of BOLD signal 4–7 s post-target). (*A*) Display of independently defined regions of interest in DMN, DAN, and PPA. (*B*) Evoked responses in DMN, DAN, and PPA were all significantly >0. Only PPA exhibited greater evoked response to correct versus lapse trials (correct omissions vs. commission errors). *$P < 0.05$.

centered on group-level peaks within the parahippocampal gyrus from the thresholded scene > face contrast [(26, −44, −7) and (−23, −44, −7), respectively; see Figure 3*A*].

To define the group-level DMN and DAN, preprocessed resting data was concatenated across participants and submitted to ICA using FSL's MELODIC software (http://www.fmrib.ox.ac.uk/fsl/melodic/index.html). Following automated estimation of the optimal number of components, the single components best representing the DMN and DAN were selected based on visual inspection. To define the most robust DMN regions (posterior cingulate, ventromedial prefrontal cortex, and bilateral lateral parietal cortex) and DAN regions (bilateral dorsal prefrontal cortex [frontal eye field] and bilateral intraparietal sulcus [IPS]), which were quite extensive even at stringent intensity thresholds and after applying multiple-comparisons corrections (via voxel-cluster correction as described above, as well as false discovery rate methods), we extracted the peak 200 contiguous voxels in each ROI. See Figure 3*A* for the resulting mask of 4 core DMN and 4 core DAN regions.

Lapse Precursors

To evaluate lapse precursors, ongoing activity during the TR preceding target (mountain) appearance was estimated separately for lapse and correct trials in PPA, DAN, and DMN regions. To isolate spontaneous signal fluctuations, these precursor analyses were conducted on the residuals of a first-stage general linear model (GLM) that accounted for signal variance associated with mean evoked response for each trial type, as well as trial-to-trial RT. This model also included terms for signal mean and linear drift, along with 8 nuisance regressors (6 realignment parameters, mean signal from spherical ROIs centered in deep white matter and lateral ventricle cerebrospinal fluid). While this "cleaning" procedure minimally influenced estimation of lapse precursors, it nonetheless ensured that precursor results were independent of incidental effects of trial order (see Fig. 4 for illustration of the procedure). Linear time interpolation was conducted to estimate the blood oxygen level–dependent (BOLD) response at each image transition (rate of 0.8 s), assuring that any interpolated response only considered the nearest TRs for estimation. BOLD signal values were averaged across a pretrial window spanning 1.6 s (2 trials) prior to target appearance. To examine whether lapse precursors differed in our 2 variability-defined attentional states, ongoing activity was evaluated separately for "in the zone" and "out of zone" trials.

Variance Time Course

BOLD effects attributable to trial-by-trial RT variability were isolated via a stagewise regression procedure similar to that described above. An initial GLM accounted for signal variance associated with mean evoked response for each trial type, trial-to-trial RT, and nuisance regressors (see above). The RT variability analysis was run on the residuals of this first-stage model, and implemented via amplitude modulation regression using the nonsmoothed VTC convolved with a 1-parameter gamma variate hemodynamic response function (HRF). The results of this analysis are presented in the main text. Two additional analyses, 1 using the nonsmoothed VTC and 1 using the smoothed VTC, each shifted 6 s to account for hemodynamic delays, were performed without HRF convolution to evaluate the temporal correlation between BOLD signal and RT variability in the absence of assumptions about response shape and duration. These 3 implementations of the VTC analysis yielded highly similar results (Fig. 6 and Supplementary Fig. 2).

Results

Behavioral Performance

Run Order Effects

To determine if there were cumulative load effects on gradCPT performance, we explored whether any dependent measure (RT, RT coefficient of variation, lapse rate, and omission error rate) or vigilance decrements in any of these measures, differed across the 3 runs. Recall that we attempted to reduce such effects through providing a rest or anatomical scan between gradCPT runs. Separate analyses of variances for each measure were conducted with run as a factor. There was a main effect of run on omission error rate ($F_{(2,30)} = 4.42$, $P < 0.05$) and mean RT ($F_{(2,30)} = 13.8$, $P < 0.001$), such that omission errors decreased across run (mean error rate in runs 1–3: 4.3%, 3.1%, and 1.2%) and mean RT decreased (780, 753, and 715 ms). In addition, decrements in RT coefficient of variation differed across runs ($F_{(2,30)} = 4.02$, $P < 0.05$), such that decrements over time were more pronounced in runs 1 and 2 than run 3. Thus, performance showed subtle improvements over time, suggesting that we were successful in eliminating cumulative load. The subsequent behavioral results are collapsed across runs for simplicity and to minimize the number of comparisons performed, despite the fact that this should, if anything, weaken estimation of vigilance decrements.

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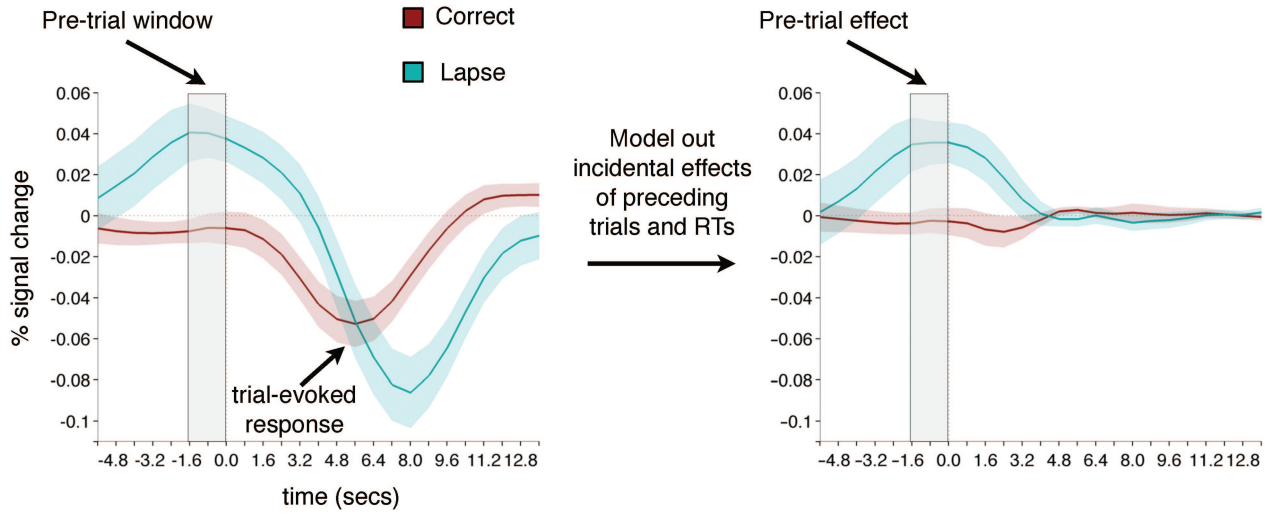

Figure 4. Illustration of lapse-precursor analysis. To isolate intrinsic activity preceding each target event from the incidental effects of prior trials, evoked responses were modeled and removed from the time course.

Accuracy

As described in the Methods section, participants viewed a stream of gradually changing scene images (Fig. 1*A* and Supplementary Movie 1), and were instructed to respond to city scenes (90%) and withhold responding to infrequent mountain scenes (10%). On average, participants made lapses (commission errors) on 26% of mountain scenes (failing to inhibit responses to mountain scenes; range: 10–49%), and made omission errors on 3% of city scenes (failing to respond to city scenes; range 0–10%).

Vigilance Decrements

Across the 8-min runs, participants exhibited significant vigilance decrements in multiple dependent measures, indicating that the gradCPT sufficiently taxes sustained attention. The rate of lapses increased over time ($t_{15} = 3.30$, $P < 0.01$, Fig. 1*C*), as did correct RT coefficient of variation (SD/mean; $t_{15} = 5.42$, $P < 0.001$, Fig. 1*D*), omission errors ($t_{15} = 2.36$, $P < 0.05$, Fig. 1*E*), and mean correct RT ($t_{15} = 2.19$, $P < 0.05$, Fig. 1*F*).

RT Variability

Across subjects, we observed a robust relationship between correct RT variability and lapse rate, with more variable subjects lapsing more frequently ($r = 0.70$, $P < 0.01$; Fig. 1*B*). Importantly, this relationship existed independent of the contribution of overall RT (semipartial $r = 0.63$, $P < 0.01$). RT was only weakly related to lapses ($r = -0.33$, $P = 0.11$; semipartial $r = -0.37$, $P = 0.08$). These results suggest that response stability is strongly and uniquely associated with the ability to sustain attention to task goals and resist lapses.

To examine within-subject fluctuations in RT stability, we computed VTCs for each participant and run (see Methods section; Fig. 2*A*). The VTC divides each run into stable epochs ("in the zone") and unstable epochs ("out of the zone"), based solely on correct responses on baseline trials. Participants made fewer errors during low variability "in the zone" epochs (see Methods section), than during high variability "out of the zone" epochs (lapse rate: $t_{15} = 6.61$, $P < 0.0001$; omission error rate: $t_{15} = 4.00$, $P < 0.01$; Fig. 2*B*). Further, when "out of the zone", participants were significantly faster preceding lapses ($t_{15} = 5.48$, $P < 0.0001$) and slower preceding correct trials ($t_{15} = 4.16$, $P < 0.001$), compared with when "in the zone" (see Fig. 2*B*). Average RT, on the other hand, was nearly identical (744 ms when "in the zone" vs. 747 ms when "out of the zone"). These findings demonstrate that the degree to which one is "in the zone" or "out of the zone" interacts with other behavioral measures, with "out of the zone" periods marked by more variable correct RTs (by definition), greater likelihood of errors, and greater influence of local response speeding or slowing on subsequent performance accuracy.

fMRI: Networks and Regions of Interest

Three sets of regions were independently defined: DAN, DMN, and bilateral PPA. DAN regions, which included putative frontal eye fields and intraparietal sulcus bilaterally (see Fig. 3*A*), exhibited a task-positive evoked response to targets (mountains) in the main task, as did PPA (*t*-tests of evoked responses vs. 0, DAN: $t_{15} = 6.34$, $P < 0.001$; PPA: $t_{15} = 5.96$, $P < 0.001$; see Fig. 3*B*). In addition, PPA exhibited greater evoked responses to correct than lapse trials ($t_{15} = 2.31$, $P < 0.05$). DMN regions, which included ventromedial prefrontal cortex, posterior cingulate, and lateral parietal cortex bilaterally (see Fig. 3*A*), exhibited task-negative, evoked deactivation to targets in the main task ($t_{15} = 4.86$, $P < 0.001$; see Fig. 3*B*). Patterns of activation and deactivation were consistent across individual regions of DAN and DMN (Supplementary Fig. 1*A*,*B*).

fMRI: Precursors of Attention Lapses

To probe the relationship between ongoing brain activity and lapses in attention, we compared BOLD signal preceding lapse trials and correct trials (failing to inhibit vs. correctly inhibiting a response) in the 3 sets of brain regions. This analysis revealed higher activity levels preceding correct trials than lapses in DAN and PPA, while the opposite pattern was observed in DMN ($t_{15} = 2.68$, $P < 0.05$ for DAN; $t_{15} = 2.50$, $P < 0.05$ for PPA; $t_{15} = 3.28$, $P < 0.01$ for DMN; see Fig. 5*A*). This pattern of results was consistent across all individual regions of each network (Supplementary Fig. 1*C*,*D*). Thus, lower pretarget activity in attentional control and scene-selective regions, and higher pretarget activity in default regions, foreshadows attention lapses.

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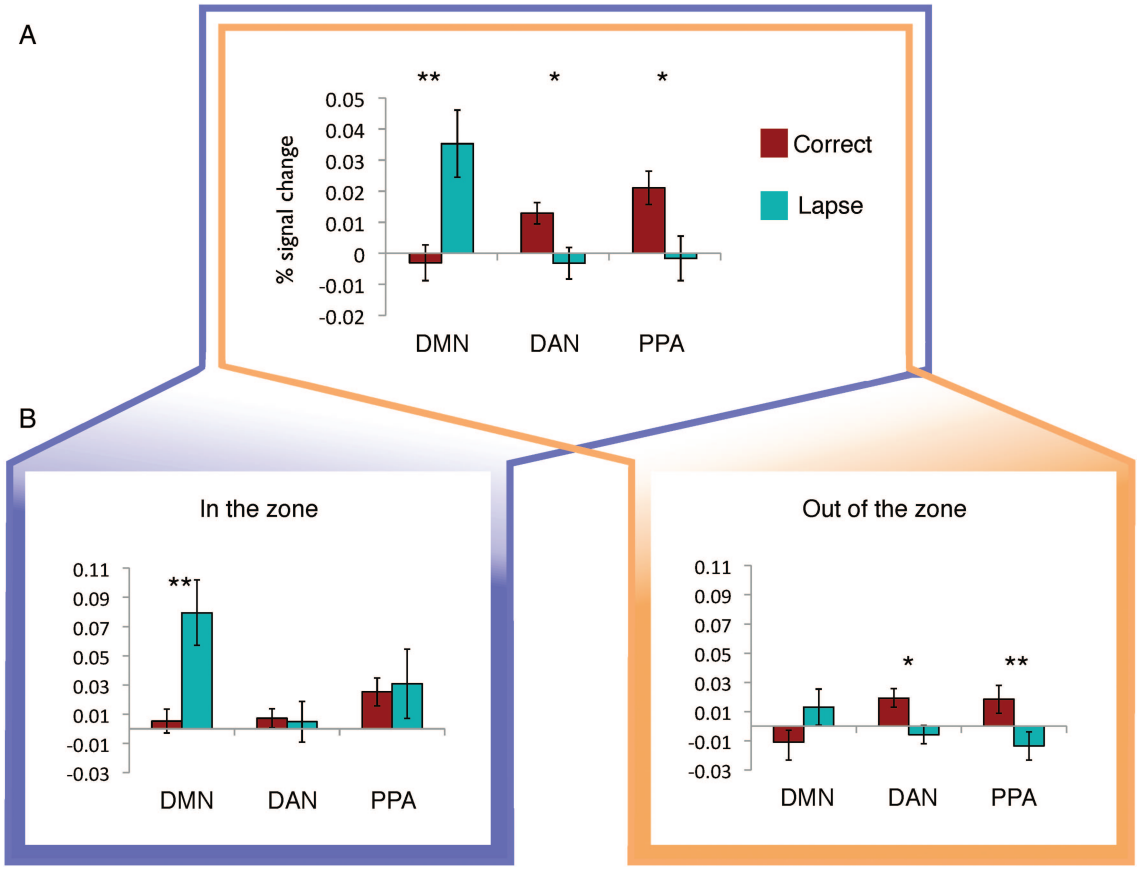

Figure 5. Precursors of attention lapses. (*A*) Overall, attention lapses (commission errors) were preceded by higher activity in DMN and lower activity in DAN and PPA compared with correct trials (correct omissions). (*B*) When "in the zone", lapses were preceded by higher DMN activity. In contrast, when "out of the zone", lapses were preceded by lower activity in DAN and PPA. $*P < 0.05$. $**P < 0.01$.

fMRI: Precursors of Attentional Lapses During Periods of Low and High RT Variability

Our behavioral results highlighted the relationship between RT variability and error- likelihood, and raised the possibility that erratic "out of the zone" and stable "in the zone" periods represent distinct attentional states. We thus speculated that the observed associations between ongoing brain activity and lapse-proneness might differ depending on whether subjects were "in the zone" or "out of the zone". To investigate this possibility, we explored the relationship between pretarget activity and subsequent attention lapses, separately for "in the zone" and "out of the zone" periods. When subjects were "in the zone", lapses were preceded by elevated DMN activity, while performance was unrelated to DAN or PPA activity ($t_{15} = 3.62$, $P < 0.01$ for DMN; $P > 0.7$ for control/PPA; See Fig. 5*B*). When subjects were "out of the zone", reduced activity in DAN and PPA preceded lapses ($t_{15} = 2.27$ and 3.24, respectively, $P < 0.05$; See Fig. 5*B*), while the effect in DMN was only marginally significant ($t_{15} = 1.80$, $P > 0.09$). Thus, lapses associated with high DMN activity were apparent primarily when subjects were "in the zone", while reliance on task-positive networks for successful inhibition was observed solely when subjects were "out of the zone". As a final note, despite observed differences in ongoing activity during "in the zone" and "out of the zone" periods, functional connectivity within- and between DMN and DAN networks (as measured by time series correlations) did not distinguish between these 2 attentional states.

fMRI: Correlates of RT Stability

To examine the neural correlates of trial-to-trial fluctuations in RT stability, whole-brain multiple regression was performed for each subject using the VTC as a regressor (see Methods section). Several regions of the DMN, including posterior cingulate, ventromedial prefrontal, and left lateral parietal cortex showed higher activity levels during moments of relative stability (see Fig. 6*A* and Table 1). Each of these DMN regions demonstrated overlap with the independently defined resting DMN (Fig. 6*C*). This VTC correlation analysis also revealed an association between RT stability and BOLD signal in the basal ganglia, suggesting a potential subcortical source of motor control associated with less variable responding. In alternate implementations of this analysis (see Methods section; Supplementary Fig. 2), a cluster in right frontoinsular cortex was positively correlated with RT variability; this region did not survive multiple comparisons correction in the main analysis, though was apparent at less stringent thresholds.

To further characterize the relationship between DMN activity and RT stability, we examined BOLD response for baseline trials when "in the zone" (low variability) and "out of the zone" (high variability) using the independent rest-defined DMN. As illustrated in Figure 6*B*, greater DMN activity

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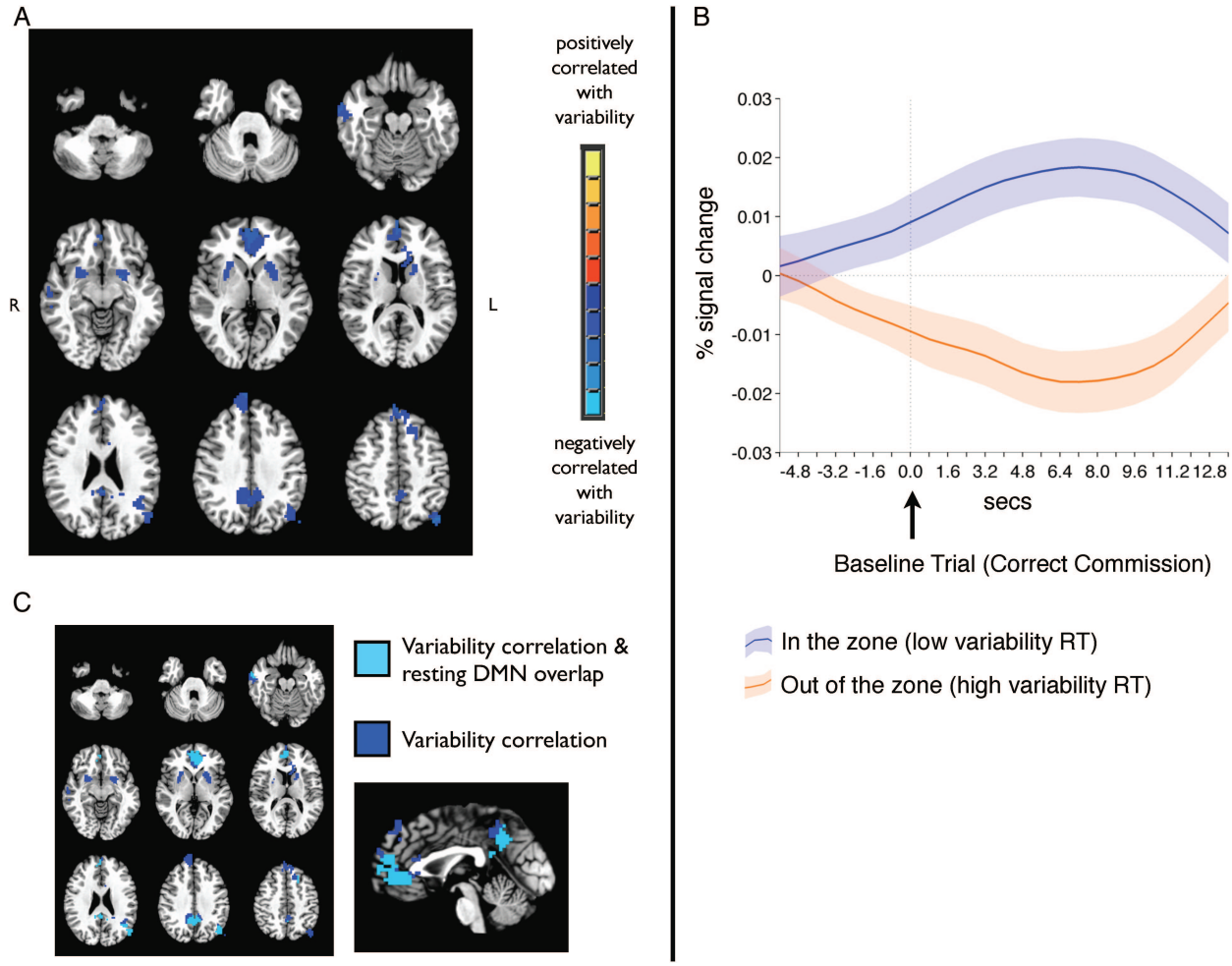

Figure 6. Reaction time stability: BOLD signal correlation. (*A*) VTC correlated negatively with several regions of DMN, such that higher DMN was associated with lower variability (more stable performance). Maps are displayed after correction for multiple comparisons (corrected $P < 0.05$; nominal $P < 0.01$, cluster size >54 voxels). (*B*) Independently defined DMN time course reveals greater activity during stable epochs ("in the zone") relative to more variable epochs ("out of the zone") as time locked to baseline (correct commission) trials. (*C*) Overlap between VTC correlation map (Figure 6*A*) and resting-state defined DMN. Dark blue indicates significant activations in VTC correlation map. Light blue indicates regions that overlapped between rest-defined DMN and VTC.

precedes and persists following less variable responses, with correct responses during low-variability periods associated with positive DMN signal, and correct responses during high-variability periods associated with negative DMN signal—DMN suppression or deactivation. The difference between low- and high-variability trials reaches its maximum ~6–8 s postresponse, validating the observed DMN variability correlation observed at the whole-brain level (Fig. 6*A*).

Results of the whole-brain VTC correlation analysis were virtually identical when we did not include trial-by-trial RT as a regressor in a first-stage GLM, suggesting that the regions identified do not also share a relationship with fluctuations in RT. To address directly whether overall RT varied with unique brain regions, we performed a parallel regression analysis with trial-by-trial RT rather than variability (Supplementary Fig. 3). This analysis revealed a distinct set of regions positively correlated with response speed, including several regions of the DAN. Positive correlations with RT (i.e. greater response associated with slower trials) potentially reflect time-on-task effects. No regions showed a negative correlation with RT. These results provide confirmation that regions showing a relationship with variability are indeed distinguishable from those showing a relationship with RT.

Thus, it appears that RT stability shares a unique trial-by-trial relationship with co-occurring fluctuations in DMN BOLD signal. The direction of this relationship reveals that increasing variability is associated with decreasing DMN activity.

Table 1

Regions significantly correlated (negatively in all cases) with RT variability (variance time course, see Methods section, Fig. 6*A*)

Region	Talairach coordinates		
B anterior medial frontal gyrus/ACC	4	49	3
B anterior superior frontal gyrus	2	43	43
L putamen	−24	5	0
B posterior cingulate/precuneus	0	−48	33
L angular gyrus	−43	−68	36
R putamen	25	6	0
L anterior superior frontal gyrus	−16	26	46
R middle temporal gyrus	58	−8	−16

Talairach coordinates indicate the center of mass of each cluster. $P < 0.05$ corrected threshold (nominal $P < 0.01$, minimum cluster size of 54 contiguous voxels).

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Discussion

We developed a novel paradigm to more sufficiently tax sustained attention through reducing the abrupt onsets and discrete trials characteristic of many CPTs. Using the gradCPT, we observed performance declines in multiple measures across an 8-min period, as well as moment-to-moment fluctuations in performance that were yoked to the ebb and flow of ongoing activity in the DAN and DMN. Specifically, moderate DMN activity accompanied less variable, less error-prone periods of performance, or being "in the zone", and the neural precursors of attention lapses (commission errors) differed when participants were "in the zone" and "out of the zone". When "in the zone", extreme peaks in DMN activity were predictive of subsequent lapses; in contrast, when out of the zone, reduced activity in DAN and task-relevant sensory regions predicted lapses. These results will be discussed in relation to existing theories of DMN and DAN functioning and sustained attention, and will form the basis of a new proposal that integrates seemingly disparate reports in the literature.

Taken together, our results reveal nuanced relationships between performance measures and ongoing brain activity that challenge current characterizations of DMN and DAN functioning. Rather than simply representing "off-task" processing that interferes with performance, we found evidence of both beneficial and detrimental effects of DMN activity, in that higher activity accompanied periods of stable, less error-prone responding, but was also foretelling of lapses. In contrast, ongoing DAN activity was predictive of subsequent lapses only during periods of high variability, challenging the notion that DAN activity represents "on-task" processing that universally aids performance. We instead propose a more flexible framework that acknowledges the influence of task demands and momentary attentional states on network recruitment.

Turning first to our DMN results, we suggest that activity levels within this network may roughly gauge the degree of cognitive effort exerted at a given moment, with more effortful performance marked by greater deactivation of DMN (i.e. more negative BOLD signal). This interpretation aligns well with the widely reported phenomenon of greater task-evoked deactivation with increasing task difficulty (e.g. McKiernan et al. 2003, 2006), as well as with findings of greater deactivation during performance of novel than practiced tasks (Mason et al. 2007; Jolles et al. 2010). In the gradCPT, error-prone and variable "out of the zone" periods may represent moments of greater subjective challenge, during which participants effortfully suppress DMN activity as they struggle to maintain task focus. In contrast, "in the zone" periods may represent moments of more automatic performance, during which correct responses are made with less effortful control, and DMN activity concomitantly rises. The observation of greater bilateral putamen activity during these periods lends further support to this account, as basal ganglia involvement generally increases as performance becomes more practiced and automatic (Hazeltine et al. 1997; Penhune and Doyon 2002). However, given that some degree of effort is clearly necessary to sustain task-relevant processing, reduction of effort beyond a critical threshold is likely to have adverse consequences. This is precisely what we found in our analysis of lapse precursors; an increase in DMN activity beyond the moderate level characteristic of "in the zone" periods was associated with subsequent attention lapses. These more dramatic elevations may represent mind-wandering or stimulus-independent processing, functions that have previously been ascribed to the DMN and shown to precede errors (McGuire et al. 1996; McKiernan et al. 2006; Mason et al. 2007; Christoff et al. 2009). In terms of the current framework, these functions exemplify the absence of cognitive effort, as they are carried out in a relatively automatic fashion, and may represent an extreme expression of the effortless state that generally aids performance on the gradCPT.

In reconciling our findings with previous reports that DMN suppression benefits performance (Daselaar et al. 2004; Marsh et al. 2006; Park et al. 2010), it is helpful to consider the unique features of our task. To adequately tax sustained attention, we created a task that was challenging because of its continuous though relatively low cognitive demand. That is, discriminating between city and mountain scenes is not difficult in itself, but maintaining the focus necessary to do so continuously is. By introducing gradual transitions between stimuli and not incorporating inter-trial intervals, participants were less able to attend only during the active trial period and then disengage between trials. Instead, the gradCPT encourages more consistent, sustained effort. This may stand in contrast to other cognitive paradigms, which permit reliance on more effortful and resource-draining mechanisms than can be replenished between trials. It may be that in the short term, when afforded periodic "rest" intervals, effortfully suppressing DMN activity benefits performance. However, when faced with continuous demands on endogenous attention, DMN suppression is not sustainable and undermines stability, thus encouraging an alternative stance that allows DMN activity to hover near baseline levels. DMN suppression during the gradCPT may thus represent a heightened commitment of resources toward the current trial at the cost of maintaining attentional resources for upcoming trials, an effect analogous to models of the attentional blink, in which detection of targets in rapid temporal succession is impaired due to "overinvesting" attentional resources on the first target (Olivers and Nieuwenhuis 2005). Correspondingly, reduced DMN suppression during "in the zone" periods may reflect a more distributed attentional state, similar to that which is enhanced by meditation practice and hypothesized to underlie the reduced attentional blink in experienced practitioners (Slagter et al. 2007; van Leeuwen et al. 2009). While speculative, we posit that this state parallels the experience of "flow" (Csíkszentmihályi 1991); rather than representing a loss of focus, it entails a sense of full immersion, a synching of self with task, during which high-level performance is achieved with relative ease. This state may also emerge during conditions of broad external awareness (Gilbert et al. 2006, 2007), insight-based problem solving (Subramaniam et al. 2009), associative thought (Bar 2007), and self-projection (Buckner and Carroll 2007)—a diverse set of thought processes believed to be supported by the DMN. Optimal performance in each of these conditions may entail a degree of task transcendence, perhaps akin to the notion of "non-striving" in meditation practice, a state that cannot be achieved through effortful control or application of analytical, linear, evaluative strategies.

The account that we have detailed thus far, in which DMN suppression accompanies effortful performance, and is not sustainable in a continuous task such as the gradCPT, provides a backdrop for understanding our findings regarding

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the DAN. It is only during these periods of effortful performance, when one is struggling to maintain task focus ("out of the zone"), that enhanced DAN activity is needed to prevent attention lapses. Thus, greater attentional control is not better across the board; rather, control mechanisms are flexibly deployed to support performance during moments of greatest challenge. Likely reflecting intensification of top-down influences on visual processing, we also found that greater ongoing PPA activity during "out of the zone" periods protected against subsequent lapses. Collectively, our results suggest that lapses during periods of poor performance result from reduced attentional control (decreased DAN and PPA activity), whereas lapses during periods of more stable and accurate performance result from over-adaptation to an effortless state (increased DMN activity).

Our findings and proposed framework of DMN and DAN functioning lend support to both of the dominant theories of sustained attention. When "in the zone", or when the task is presumably less challenging and performed more automatically, lapses are preceded by elevated DMN activity—in line with the mindlessness or "underload" model. On the other hand, during more demanding epochs, lapses are associated with failures to fully engage task-positive DAN regions associated with attentional control. This less consistent deployment of attentional control during "out of the zone" periods may be a reflection of resource depletion—in line with an "overload" model. Although a direct neural correlate of overall vigilance declines is not accessible with BOLD fMRI due to reduced signal-to-noise for such low-frequency changes, the fact that "out of the zone" epochs are more prevalent later in task runs (Fig. 2*C*) suggests that depletion of attentional resources may increasingly contribute to failures as the task progresses. Thus, lapses due to underload and overload appear to occur at different times, and these 2 explanations of sustained attention failures need not be considered mutually exclusive.

The current results encourage models of DMN and DAN functioning and sustained attention that move beyond simple dichotomies. Promising avenues for future inquiry include the influence of task features on performance and neural recruitment (e.g. the "stop and go" of discrete trial designs versus more continuously demanding tasks), and the sophisticated interplay between ongoing brain activity and local cognitive states (e.g. individually defined periods of greater and lesser challenge identified by trial-by-trial performance or physiological measures such as pupillometry). In fact, differences in task features and performance markers examined (e.g. slow responses, errors, self-reported mental state, and trial-by-trial fluctuations in flexibility and distractibility) might in part explain disparate findings regarding the functional implications of ongoing DMN and DAN activity. Our results underscore the importance of considering such factors, as within a single task we observed differing influences of DMN and DAN activity across 2 behavioral markers (variability and lapse-likelihood), as well as effects that were sensitive to subtle shifts in attentional state (in vs. "out of the zone").

We have interpreted the observed within-subject fluctuations in variability in the context of previous work linking individual differences in RT variability to disorders of attention, executive function, and impaired or inefficient functioning of DAN and DMN. Despite this wealth of evidence connecting performance variability to attentional control, we acknowledge the possibility that low variability epochs represent states in which motor response settings are optimized to balance speed-accuracy trade-offs. In contrast, high-variability epochs may reflect periods in which these response settings are nonoptimal, or speed-monitoring fails (Rabbitt and Vyas 1969). These possibilities are not mutually exclusive, in that sustainable states of attention may be functionally related to optimized response settings or monitoring. Further, when these settings are not optimized, the task may be experienced as more effortful, prompting adjustments of one's approach. While it is not possible to fully disentangle these 2 explanations for "in the zone" and "out of the zone" states, the finding of increasing prevalence of "out of the zone" periods with time on task (Fig. 2*C*) is most consistent with an attentional interpretation. That is, exploration of motor settings would likely occur early on, when one is less familiar with the task, whereas demands on attentional control are expected to mount with time.

The present findings have wide-ranging implications. The ability to maintain stable attentional engagement provides the foundation for higher-order operations such as memory, decision making, and action selection, suggesting that future studies across multiple cognitive domains and paradigms might benefit from our methods for measuring background attentional state. As the neural systems supporting task performance appear to shift with one's attentional state, failure to account for attention fluctuations may obscure meaningful information about underlying mechanisms. Extension of these findings to clinical populations will also be informative. One intriguing possibility is that an inability to flexibly regulate cognitive effort to achieve task goals is a unifying feature across the diverse populations in which DMN dysfunction has been observed (including ADHD, autism, Alzheimer's, schizophrenia, and affective disorders; see Broyd et al. 2009; Fornito et al. 2010 for reviews). We hope that our preliminary framework, along with other recent studies that paint a complex picture of DAN and DMN (Hasson et al. 2009; Gerlach et al. 2011; Prado and Weissman 2011), will stimulate research beyond prevailing models, ultimately advancing our understanding of how behavior unfolds over time.

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/.

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Notes

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