

The neural bases of momentary lapses in attention

D H Weissman¹, K C Roberts¹, K M Visscher² & M G Woldorff¹

Momentary lapses in attention frequently impair goal-directed behavior, sometimes with serious consequences. Nevertheless, we lack an integrated view of the brain mechanisms underlying such lapses. By investigating trial-by-trial relationships between brain activity and response time in humans, we determined that attentional lapses begin with reduced prestimulus activity in anterior cingulate and right prefrontal regions involved in controlling attention. Less efficient stimulus processing during attentional lapses was also characterized by less deactivation of a 'default-mode' network, reduced stimulus-evoked sensory activity, and increased activity in widespread regions of frontal and parietal cortex. Finally, consistent with a mechanism for recovering from attentional lapses, increased stimulus-evoked activity in the right inferior frontal gyrus and the right temporal-parietal junction predicted better performance on the next trial. Our findings provide a new, system-wide understanding of the patterns of brain activity that are associated with brief attentional lapses, which informs both theoretical and clinical models of goal-directed behavior.

Momentary lapses in attention can disrupt goal-directed behavior numerous times each day¹. In most cases, the results are fairly benign, such as responding more slowly to a behaviorally relevant stimulus² or forgetting what we planned to do next³. In some cases, however, more serious consequences are involved, such as traffic accidents⁴ and work-related injuries¹. Brief attentional lapses also disrupt goal-directed behavior in clinical syndromes such as attention deficit and hyperactivity disorder^{2,5}. Despite the prevalence of attentional lapses in everyday life, we have yet to develop a system-wide understanding of the brain mechanisms underlying them.

Biased-competition models of attention provide important clues regarding the neural bases of brief attentional lapses. According to such models, frontal regions of the brain that control attention (that is, frontal control regions) bias sensory regions to favor the processing of behaviorally relevant stimuli over that of irrelevant stimuli^{6–9}. This biasing increases sensory cortical activity that is evoked by behaviorally relevant stimuli^{10,11}, resulting in high-quality perceptual representations that can be fed forward to other brain regions that determine behavior⁶.

Given such models, we investigated whether brief attentional lapses originate from momentary reductions of activity in frontal control regions just before a behaviorally relevant stimulus is presented. We further predicted that reduced prestimulus activity in frontal control regions would lead to system-wide changes in stimulus-evoked activity during task performance, reflecting impairments in suspending irrelevant mental processes¹², forming high-quality perceptual representations of behaviorally relevant stimuli⁶, identifying and responding to relevant stimuli¹³, and minimizing distraction from irrelevant stimuli^{14–17}. Finally, we investigated whether a ventral fronto-parietal network previously implicated in reorienting attention¹⁸ helps us to recover from brief attentional lapses.

To investigate these hypotheses, we asked study participants to perform a global/local selective-attention task^{19–21} while we recorded their response time in each trial along with their brain activity (using event-related functional magnetic resonance imaging (fMRI)). In each trial, participants identified either the large, global letter or the small, local letters of a hierarchically organized visual object (**Fig. 1**). In psychophysical experiments, brief attentional lapses of varying magnitude contribute to variability in response time across trials^{2,22}. Therefore, we defined brief attentional lapses as relatively slow response times to identify behaviorally relevant stimuli. Our findings confirmed all of our hypotheses and provide a new, system-wide view of the neural bases of momentary lapses in attention.

RESULTS

Overall behavior

Participants performed the global/local selective-attention task very accurately (mean error rate, 3.28%). Consistent with previous findings indicating that it is harder to identify an object's local parts than its global shape²⁰, mean response time (RT) was significantly slower when participants identified the local letters than when they identified the global letters (651 ms versus 573 ms; $F_{1,15} = 20.76$, $P < 0.001$); however, this effect did not achieve significance in the error rates: $F_{1,15} < 1$). Also as previously reported²⁰, performance was significantly worse when the global and local letters in a stimulus were mapped to conflicting responses (incongruent stimuli) than when they were mapped to the same response (congruent stimuli), both for mean RT (630 ms versus 594 ms; $F_{1,15} = 45.819$, $P < 0.001$) and, marginally, for mean error rate (3.80% versus 2.76%; $F_{1,15} = 4.426$, $P = 0.053$). No other behavioral effects were significant.

¹Center for Cognitive Neuroscience and Department of Psychiatry, Duke University, Durham, North Carolina 27708, USA. ²Volen Center for Complex Systems, Brandeis University, Waltham, Massachusetts 02454, USA. Correspondence should be addressed to D.H.W. (weissman@duke.edu).

Received 8 February; accepted 24 May; published online 11 June 2006; doi:10.1038/nn1727



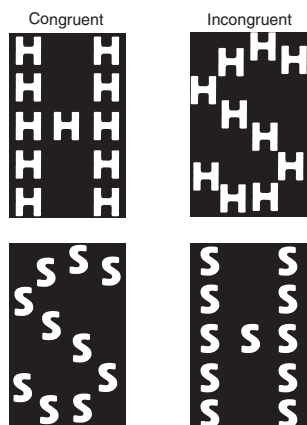


Figure 1 Experimental stimuli used in the global and local tasks. In different blocks, participants pressed a button as quickly and accurately as possible to indicate the identity (H or S) of the large, global letter or the small, local letters of a hierarchically organized visual stimulus (for example, a large H made up of small Hs). In half the trials, the global and local letters were mapped to the same response (congruent trials; for example, a large H made of small Hs); in the other half, they were mapped to different responses (incongruent trials; for example, a large H made of small Ss). In the actual experiment, a red fixation dot was displayed at the center of the screen throughout each run, and the experimental stimuli appeared briefly surrounding the dot.

fMRI

For each participant, we used multiple linear regression to derive the time course of the average fMRI response associated with each trial type²³. Critically, for each time point of these derived responses, our model estimated how much the fMRI response on an individual trial deviated from the average fMRI response for that trial type, as a function of the amount of time that the RT on an individual trial deviated from the mean RT for that trial type (Methods). This estimate was calculated in units of percent change in fMRI signal per second of increased RT above the mean RT. With only a few noted exceptions, after estimating the relationship between longer RTs and fMRI signal separately for each trial type, we averaged these estimates across all trial types (that is, all global and local stimuli) to investigate the most general linear relationships between longer RTs and target-related activity. Furthermore, we used

Figure 2 Relatively small amounts of prestimulus activity in frontal control regions predict relatively slow response times. (a) A statistical map indicating voxels in the anterior cingulate cortex (ACC), right middle frontal gyrus (MFG) and right inferior frontal gyrus (IFG), where slower RTs were associated with reduced activity one time point (that is, 1.25–2.5 s) after stimulus onset. These activations are overlaid on several slices of the MNI-normalized brain. In this and subsequent figures, coordinates in parentheses refer to the center of mass in Talairach space. (b) The relationship between longer RTs and target-related activity (in units of percent change in fMRI signal per second of increased RT above the mean RT) across time in the ACC. Notice that fMRI activity one time point before stimulus onset decreases as RT increases. Furthermore, this negative relationship between longer RTs and target-related activity reaches its minimum value one time point after stimulus onset (arrow). This gradual decrease is highly consistent with a momentary reduction of neural activity that occurs during the intertrial interval before a stimulus is presented, and achieves its peak hemodynamic effect 3.75–6 s later. (c) The average fMRI response to target stimuli (in units of percent change from baseline) across time in the ACC.

random-effects statistical analyses so that our results would generalize to the population.

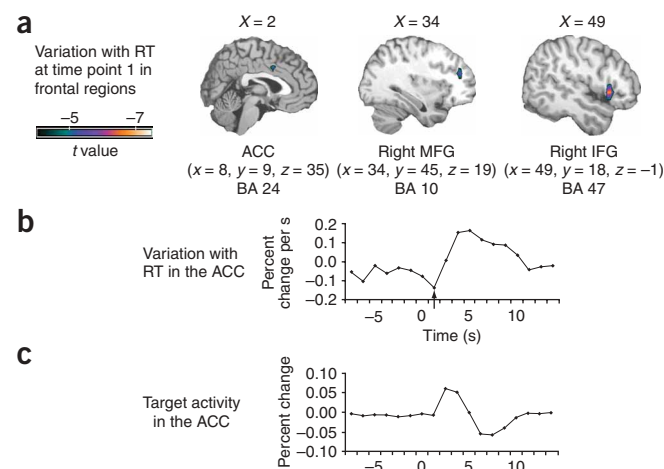
Reduced early activity in control regions predicts lapses

We hypothesized that brief attentional lapses stem from momentary reductions of activity in frontal control regions just before a target stimulus is presented. This view predicts that trials preceded by relatively small amounts of fMRI activity in frontal control regions should be associated with relatively long RTs. In the present study, the average intertrial interval lasted approximately 3.75 s, and, owing to the sluggishness of the hemodynamic signal measured with fMRI, the peak hemodynamic response to a neural event typically occurred 3.75–6.25 s after that event. Thus, a momentary lapse in attention that began after the response was made in one trial should, on average, produce its peak hemodynamic effect 0–2.5 s after the onset of the next target stimulus. Some effects might also be observed just before the onset of the next stimulus, but these would probably be smaller owing to the hemodynamic response delay.

Consistent with predictions, in several cortical regions longer RTs were associated with reduced target-related activity ($t_{15} = -4.07$, $P < 0.0005$, 5 contiguous voxels) 1.25–2.5 s after stimulus onset (Fig. 2a,b). These regions included the right inferior frontal gyrus (IFG), thought to participate in stimulus-triggered reorienting of attention¹⁸, the right middle frontal gyrus (MFG), thought to maintain task goals in working memory^{24–26}, and the anterior cingulate cortex (ACC), thought to detect and/or resolve processing conflicts^{13,17}. Considering the approximate 2-s delay between an event and the first discernible fMRI signal in response to that event²⁷, this reduced activity 1.25–2.5 s after stimulus onset probably reflects attentional lapses that occurred before trial presentation.

In further support of this conclusion, more powerful region of interest (ROI) analyses (Methods) revealed that in both the right IFG and the ACC, longer RTs were also associated with reduced target-related activity 0–1.25 s after stimulus onset (IFG: $t_{15} = 2.21$, $P < 0.022$; ACC: $t_{15} = 1.85$, $P < 0.043$). Moreover, an analogous effect occurred in the right IFG 1.25–0 s before stimulus onset ($t_{15} = 2.20$, $P < 0.022$). These findings provide additional evidence that the effects in frontal control regions resulted from attentional lapses before trial presentation.

Finally, longer RTs were also associated with greater peak activity in these same regions of the right IFG ($t_{15} = 3.95$, $P < 0.001$), the right MFG ($t_{15} = 5.1$, $P < 0.0001$) and the ACC ($t_{15} = 3.05$, $P < 0.005$)



(Fig. 2b–c). Thus, greater control may be needed to process stimuli that are presented during momentary lapses in attention.

Lapses linked to increased ‘default-mode’ network activity

The ‘default-mode’ network^{12,28} is a set of brain regions that is thought to underlie task-irrelevant mental activities that occur during the intertrial interval, such as daydreaming or recalling previous experiences from memory. It has been proposed that when a behaviorally relevant stimulus is presented, processing resources need to be reallocated toward behaviorally relevant processes, resulting in task-induced deactivation in the default-mode network²⁹. During a brief attentional lapse, however, participants might not fully reallocate attentional resources. This view predicts that the smaller the task-induced deactivation in the default-mode network in any particular trial, the more slowly participants should respond.

To investigate this prediction, we first performed a one-way, repeated-measures analysis of variance (ANOVA) on the average fMRI response to target stimuli across time, in order to determine which regions showed task-induced deactivation (that is, voxels where the ANOVA was significant and the peak activity was less than zero). Second, we performed an analogous one-way ANOVA on the relationship between longer RTs and target-related activity across time to determine the brain regions in which longer RTs were associated with increased target-related activity (that is, voxels where the ANOVA was significant and the peak relationship between longer RTs and target-related activity was greater than zero). Third, after thresholding each voxelwise map ($F_{11,165} = 3.03$, $P < 0.001$, 5 contiguous voxels), we used a conjunction analysis to determine which voxels were activated in both maps.

As hypothesized, longer RTs were associated with increased target-related activity in several regions of the default-mode network, including the posterior cingulate cortex, the precuneus and the middle temporal gyrus (Fig. 3a and Table 1). For example, notice that for the average task-induced deactivation in the right precuneus (Fig. 3b), the relationship between longer RTs and target-related activity across time resembles a positive hemodynamic response (Fig. 3c). Thus, as predicted, longer RTs were associated with greater target-related activity (that is, smaller task-induced deactivations) in the default-mode network.

Lapses associated with reduced visual cortex activity

As described earlier, we found that reduced activity in frontal control regions predicted momentary lapses in attention. This result suggests

Table 1 Regions of a ‘default-mode’ network in which relatively large deactivations were associated with relatively fast response times

| Region | BA | X | Y | Z |
|-------------------------------|-----|-----|-----|----|
| Frontal | | | | |
| Right precentral gyrus | 4 | 30 | -26 | 64 |
| Right middle frontal gyrus | 8/9 | 34 | 24 | 40 |
| Posterior cingulate | 31 | 0 | -31 | 43 |
| Parietal | | | | |
| Right precuneus | 7 | 8 | -56 | 44 |
| Right precuneus | 7 | 8 | -55 | 58 |
| Right superior parietal lobe | 7 | 34 | -49 | 58 |
| Right inferior parietal lobe | 40 | 38 | -45 | 51 |
| Temporal | | | | |
| Right middle temporal gyrus | 19 | 49 | -80 | 18 |
| Occipital | | | | |
| Left superior occipital gyrus | 19 | -41 | -79 | 25 |

X, Y and Z indicate the center of mass in Talairach and Tournoux coordinates. BA, Brodmann area.

that attentional lapses should also be associated with reduced stimulus-triggered activity in the sensory cortices, signaling the failure of attention to enhance the formation of behaviorally relevant perceptual representations. To investigate this hypothesis, we first determined the cortical regions involved in processing our visual stimuli. Consistent with previous studies of visual attention, a one-way, repeated-measures ANOVA (with time as a factor) on the average fMRI response to all target stimuli revealed significant ($F_{11,165} > 3.7$, $P < 0.0001$, minimum cluster size 5 voxels) positive activations (that is, peak activity greater than zero) in a distributed network of brain regions (Fig. 4a). Note, for instance, the average time courses of positive target-related activity in the ACC (Fig. 4b, left) and in the left inferior occipital cortex (IOC; Fig. 4b, right).

To test our hypothesis about visual cortex, we used ROI analyses to assess the relationship between longer RTs and target-related activity within the two visual cortical regions that were most highly activated by our target stimuli (Fig. 4a, right). These ROI analyses in bilateral IOC confirmed our prediction that brief attentional lapses would be associated with reduced stimulus-evoked activity in the visual cortex. In particular, in both the left and right IOC, we observed significant negative relationships between longer RTs and target-related activity (left IOC: Talairach center of mass, $x = -30$, $y = -92$, $z = -15$; $t_{15} = -1.87$, $P < 0.05$ at the peak of the average fMRI response; right IOC: Talairach center of mass, $x = 34$, $y = -88$, $z = -15$; $t_{15} = -1.90$, $P < 0.04$, one time point before the peak of the average fMRI response). Notice that, for the left IOC, the relationship between longer RTs and target-related activity across time resembles an inverted

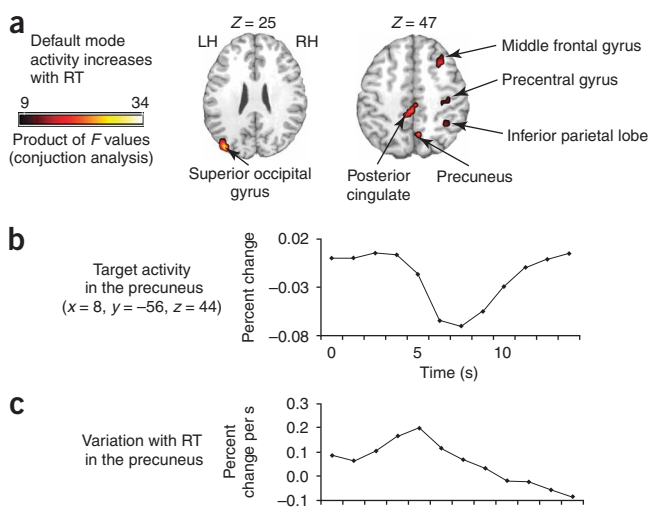


Figure 3 Smaller deactivations in the default-mode network are associated with longer response times. (a) A statistical map indicating voxels that showed both task-induced deactivation and a positive relationship between longer RTs and target-related activity, overlaid on two slices of the MNI-normalized anatomical brain. Note that we have plotted the product of the significant F -values from each statistical map, in order to highlight regions in which relatively high F -values occurred in one or both maps. LH, left hemisphere; RH, right hemisphere. (b) The average fMRI response for target stimuli in the right precuneus (in units of percent change from baseline) across time, clearly indicating a task-induced deactivation. (c) The relationship between longer RTs and target-related activity (in units of percent change in fMRI signal per second of increased RT above the mean RT) across time in the right precuneus. Note the positive relationship between longer RTs and peak target-related activity, indicating that slower RTs were associated with greater overall activity (that is, smaller deactivations).

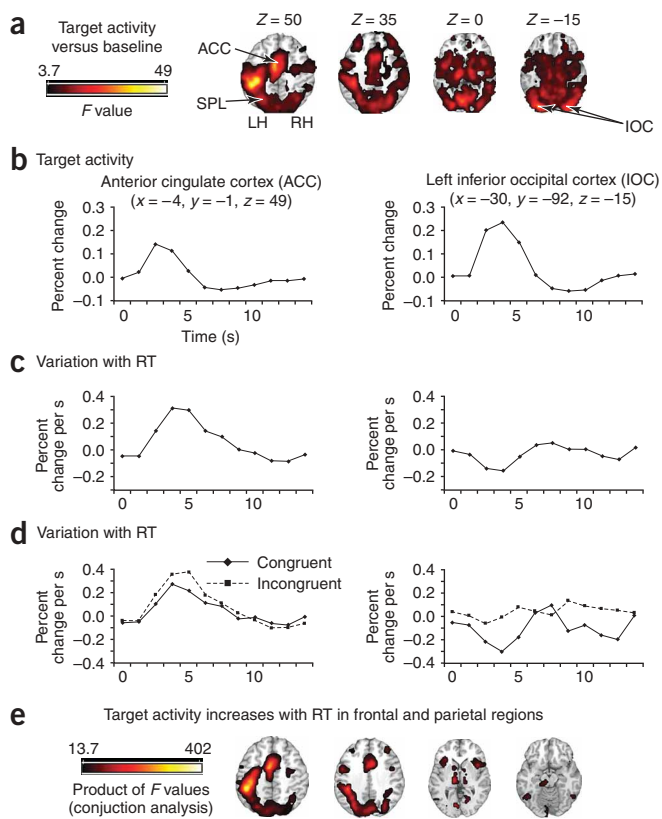


Figure 4 Relationships between longer response times and target-related activity in fronto-parietal and sensory cortices. **(a)** Target-related brain activity, plotted using F -values, overlaid on several slices of the MNI-normalized anatomical brain. LH, left hemisphere; RH, right hemisphere. **(b)** The average fMRI response for target stimuli (in units of percent change from baseline) across time in the ACC (left) and the left inferior occipital cortex (IOC; right). **(c)** The relationship between longer RTs and target-related activity (in units of percent change in fMRI signal per second of increased RT above the mean RT) across time, plotted for the ACC (left) and the left IOC (right). Notice that the relationship between longer RTs and peak activity is positive in the ACC, but negative in the left IOC. **(d)** Differential relationships between longer RTs and target-related activity across time for incongruent stimuli versus congruent stimuli in the ACC (left) and the left IOC (right). **(e)** Regions in which longer RTs were associated with increased target-related activity. The data represent the product of significant F -values from two one-way, repeated-measures ANOVAs, which assessed the average target-related activity across time and the average relationship between longer RTs and target-related activity across time. High values indicate regions where relatively large F -values occurred in one or both ANOVAs.

negative relationship between longer RTs and peak target-related activity was significantly larger for congruent than for incongruent stimuli in the left IOC ($t_{15} = -2.49$, $P < 0.015$) (this effect did not achieve significance in the right IOC ($t_{15} = -0.98$, $P > 0.17$)). These findings suggest that brief attentional lapses reduce the recruitment of a relatively general attentional mechanism such as, possibly, the allocation of spatial attention to the location of a behaviorally relevant stimulus.

Lapses increase demands on higher-order processing areas

Our finding that longer RTs were associated with reduced stimulus-triggered activity in the visual cortex is consistent with a brief interruption of top-down signals that normally bias sensory processing in favor of behaviorally relevant stimuli. If this view is correct, then brief attentional lapses should result in lower-quality perceptual representations being fed forward to downstream regions, including frontal and parietal regions that identify and respond to behaviorally relevant stimuli. These regions should then need to work harder, resulting in positive relationships between longer RTs and stimulus-triggered fMRI activity.

To test this hypothesis, we used a conjunction analysis to compare the regions that showed (i) positive activations for the average fMRI response to target stimuli across time and (ii) positive relationships between longer RTs and target-related activity across time. Positive activations in the two ANOVAs above were defined as voxels where the ANOVA was significant ($F_{11,165} > 3.7$, $P < 0.0001$, 5 contiguous voxels) and either the peak activity was greater than zero or the peak value of the relationship between longer RTs and target-related activity was greater than zero. As predicted, many of the frontal and parietal regions that showed positive activations to targets also showed significant, positive relationships between longer RTs and target-related activity (**Fig. 4e** and **Table 2**), meaning that trials with longer RTs were associated with larger fMRI responses.

Lapses impair the ability to minimize distraction

Reducing the quality of perceptual representations for a relevant target stimulus allows distracters to exert a stronger influence on performance³⁰. For incongruent stimuli, greater distracter processing should lead to greater response conflict, as the target and distracter are mapped to competing responses. For congruent stimuli, however, greater distracter processing should not lead to greater response conflict, as the target and distracter are mapped to the same response. Thus, if momentary lapses in attention reduce the quality of perceptual

(that is, negative) hemodynamic response (**Fig. 4c**, right). Thus, as predicted, longer RTs were associated with reduced stimulus-triggered sensory activity.

Lapse effects in visual cortex vary with trial type

An equivalent way to state our findings in the IOC is that greater stimulus-evoked activity was associated with faster RTs. If this result is due to better selection and processing of the task-relevant letter (but not the irrelevant letter) in some trials than in others, then it should hold equally for incongruent and congruent stimuli. In both cases, better selective processing of the relevant letter should lead to a faster response.

On the other hand, if this result is due to increased recruitment of a relatively general attentional mechanism, such as the allocation of greater spatial attention to the location of the entire stimulus, then our findings in the IOC might hold for congruent stimuli, but not for incongruent stimuli. For congruent stimuli, increased attention to both the global and the local letters should lead to faster RTs because high-quality perceptual representations of either letter should facilitate a correct response²⁴. For incongruent stimuli, however, high-quality perceptual representations of the relevant letter should lead to a fast response, whereas such representations of the irrelevant letter should lead to a slow response²⁴. Given these opposing influences, there might be weaker relationships, or even no relationships, between longer RTs and the fMRI activity evoked by incongruent stimuli in the IOC.

Consistent with a relatively general attentional mechanism, ROI analyses (**Fig. 4d**, right) revealed that the same negative relationships between longer RTs and target-related activity that we observed in bilateral regions of the IOC were significant for congruent stimuli (left IOC, $t_{15} = -3.44$, $P < 0.002$; right IOC, $t_{15} = -2.17$, $P < 0.025$), but not for incongruent stimuli (left IOC: $t_{15} = -0.098$, $P > 0.46$; right IOC: $t_{15} = -1.08$, $P > 0.14$). Furthermore, the size of the

Table 2 Major foci of target-related activations, at which greater fMRI signal was associated with relatively long response times

| Region | BA | X | Y | Z |
|---------------------------------|----|-----|-----|-----|
| Frontal | | | | |
| Left precentral gyrus | 6 | -34 | -16 | 56 |
| Left anterior cingulate cortex | 24 | -4 | -1 | 49 |
| Right anterior cingulate cortex | 24 | 8 | 12 | 34 |
| Left middle frontal gyrus | 9 | -45 | 30 | 26 |
| Right middle frontal gyrus | 9 | 38 | 41 | 26 |
| Left inferior frontal gyrus | 9 | -52 | 2 | 35 |
| Parietal | | | | |
| Left inferior parietal lobe | 40 | -41 | -35 | 43 |
| Right supramarginal gyrus | 40 | 38 | -42 | 37 |
| Left precuneus | 19 | -30 | -64 | 38 |
| Temporal | | | | |
| Left fusiform gyrus | 37 | -45 | -55 | -17 |
| Right inferior temporal gyrus | 37 | 49 | -55 | -17 |
| Left middle temporal gyrus | 37 | -52 | -62 | -4 |
| Right superior temporal gyrus | 41 | 55 | 18 | -8 |
| Occipital | | | | |
| Left lingual gyrus | 18 | -4 | -84 | -8 |
| Right cuneus | 7 | 4 | -75 | 31 |
| Insula | | | | |
| Left insula | 13 | -34 | 15 | 7 |
| Right insula | 13 | 41 | 15 | -1 |
| Subcortical | | | | |
| Left thalamus | | -11 | -18 | 1 |

X, Y and Z indicate the center of mass in Talairach and Tournoux coordinates. BA, Brodmann area.

representations for target stimuli, they should increase brain activity in regions that are sensitive to response conflict more for incongruent than for congruent stimuli.

To test this hypothesis, we performed ROI analyses in the ACC (Fig. 4a–b, left), a brain region thought to play a major role in detecting and/or resolving response conflict^{14–17}. Consistent with previous findings, the ACC (Talairach center of mass, $x = -4$, $y = -1$, $z = 49$) showed significantly greater peak activity for incongruent than for congruent stimuli ($t_{15} = 2.08$, $P < 0.03$). Moreover, as predicted, the peak relationship between longer RTs and fMRI activity (time points 4 and 5; Fig. 4c, left) was significantly more positive for incongruent than for congruent stimuli ($t_{15} = 2.15$, $P < 0.025$ (Fig. 4d, left), indicating that brief attentional lapses give rise to greater response conflict.

Recovery from lapses linked to right TPJ and IFG activity

Ventral fronto-parietal regions, including the right temporal-parietal junction (TPJ) and the right IFG, are thought to participate in signaling

Figure 5 Greater current-trial activity in the ventral fronto-parietal network predicts faster response time in the next trial. (a,b) Voxels in the right temporal-parietal junction (TPJ) and right inferior frontal gyrus (IFG) where greater peak target-related activity in the current trial predicted faster RTs in the next trial, overlaid on two slices of the MNI-normalized anatomical brain. (c) The relationship between longer RTs in the next trial and target-related activity in the current trial (in units of percent change in fMRI signal per second of increased next-trial RT above the mean next-trial RT) across time in the right TPJ. Note that greater peak target-related activity in the current trial is associated with faster RT in the next trial (arrow at time point 4, where there is a negative relationship between longer RTs in the next trial and peak target-related activity). (d) The average fMRI response for target stimuli (in units of percent change from baseline) across time in the right TPJ, which peaks at time point 4 (arrow).

the need to reorient attention toward behaviorally relevant stimuli and events¹⁸. Moreover, the appearance of a new stimulus often serves to trigger these mechanisms^{31,32}. Such findings suggest that these mechanisms might also contribute to recovering from momentary lapses in attention. For example, the appearance of a new stimulus might result in stimulus-triggered reorienting of spatial attention back to the location at which stimuli are being presented. Although such reorienting might occur too late to aid performance in the current trial, it might benefit performance in the next trial.

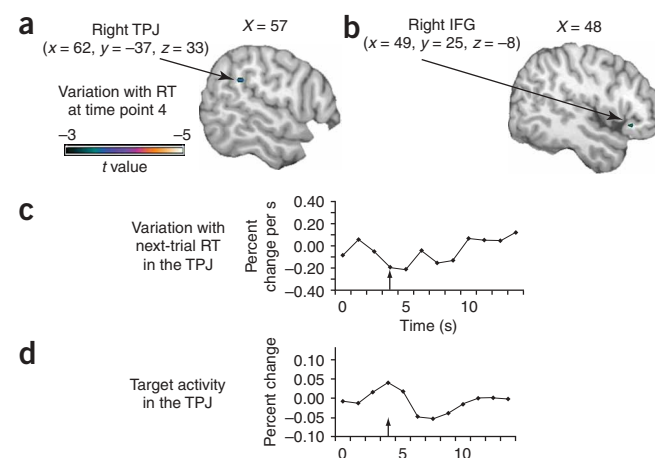
Consistent with this hypothesis, greater peak activity in the right TPJ (Fig. 5a) and the right IFG (Fig. 5b) during the current trial was associated with a faster RT in the next trial (Methods). Specifically, a t -test (restricted to right temporal-parietal and right inferior frontal cortices; threshold, $t_{15} < -3.0$, $P < 0.005$, 5 contiguous voxels) revealed significant negative relationships between peak target-related activity in the current trial and longer RTs in the next trial, both in the right TPJ (Talairach center of mass, $x = 62$, $y = -37$, $z = 33$) and the right IFG (Talairach center of mass, $x = 49$, $y = 25$, $z = 8$). For example, in the right TPJ, the relationship between longer RTs in the next trial and target-related activity in the current trial was markedly negative at time point four (Fig. 5c), which corresponds to the peak of the average fMRI response in the current trial (Fig. 5d).

Follow-up ROI analyses indicated that the significant negative relationships described above, between peak activity in the current trial and longer RTs in the next trial, were specific to RT in the next trial. In the right TPJ, there was no significant relationship between peak activity in the current trial and RT in the current trial ($t_{15} < 1$). In the right IFG, greater peak activity in the current trial was associated with slower RT in the current trial ($t_{15} = 4.15$, $P < 0.0001$, two-tailed). This result suggests that brief attentional lapses trigger the reorienting processes performed by the right IFG, which, although too late to facilitate performance in the current trial, aid performance in the next trial.

DISCUSSION

In the present study, we identified the brain regions in which brief attentional lapses originate, the effects of such lapses on brain activity related to behaviorally relevant stimuli, and the brain regions that help us to recover from such lapses.

First, consistent with biased-competition models of attention^{6–9}, we found that momentary lapses in attention are associated with reduced activity in the frontal cortex before behaviorally relevant stimuli are presented. Critically, the brain regions in which these effects occurred—the right IFG, the right MFG, and the ACC—have previously been



implicated in the control of attention. Specifically, the right IFG is thought to participate in stimulus-driven reorienting of attention¹⁸, the right MFG in maintaining and strategically manipulating the contents of working memory^{24–26}, and the ACC in detecting and/or resolving processing conflicts^{13,17}. Moreover, studies of brain-injured humans have implicated the right prefrontal cortex in sustaining attention^{33,34}. Our findings suggest that trial-to-trial variability in the efficiency of these executive processes is a major determinant of momentary lapses in attention.

Second, we found that momentary lapses in attention are associated with reduced task-induced deactivation of the default-mode network^{12,28}, suggesting less effective suspension of task-irrelevant mental processes (for example, daydreaming or monitoring the external environment). This result concurs with related findings indicating that reduced task-induced deactivation is associated with slower^{35,36} and less accurate³⁷ performance. Notably, activity in only part of the default-mode network varied with response time, suggesting that only a subset of default-mode processes interfere with task performance. Finally, because our findings indicate that momentary lapses in attention are associated with both reduced activity in frontal control regions and greater activity (that is, less task-induced deactivation) in the default-mode network, they seem related to recent reports that spontaneous activity in the attentional network is negatively correlated with spontaneous activity in the default-mode network³⁸. Specifically, our results seem to extend these findings by revealing how trial-by-trial tradeoffs of activation between the default-mode and attentional networks are related to trial-by-trial changes in behavioral performance.

Third, we found that momentary lapses in attention are associated with reduced stimulus-triggered activity in bilateral IOC. Together with the reduced activity in frontal control regions, this result seems to signal the failure of frontal control regions to fully enhance the perceptual processing of behaviorally relevant stimuli. Although numerous studies have revealed that attention modulates activity in the sensory cortices^{8,11}, we have demonstrated that sensory cortical activity correlates with response time on a trial-by-trial basis, a new result that extends related findings in nonhuman primates³⁹ to humans. Further analyses revealed that our findings in bilateral IOC were stronger for congruent than for incongruent stimuli. As discussed in the Results section, this result suggests that brief attentional lapses reduced attention to the stimulus as a whole rather than to just the task-relevant stimulus dimension. Together, these findings provide compelling evidence that momentary lapses in attention involve a reduction of top-down biasing signals to the sensory cortices, probably resulting in relatively low-quality perceptual representations of behaviorally relevant stimuli⁶.

Fourth, we found that momentary lapses in attention are associated with increased activity in higher-level brain regions that identify and respond to behaviorally relevant stimuli. This result suggests that these systems need to work harder, or longer, to complete their processing when they receive relatively low-quality perceptual representations. Notably, exactly the same frontal control regions that showed negative relationships between longer response times and target-related activity before brief attentional lapses occurred also demonstrated positive relationships after such lapses. Thus, brief attentional lapses seem to result in a compensatory recruitment of control mechanisms, which may help to cope with increased processing demands^{17,40,41}.

Fifth, we found that momentary lapses in attention increase activity in the ACC more for incongruent stimuli, which engender response conflict, than for congruent stimuli, which do not. Because the ACC is thought to make a substantial contribution to detecting and/or resolving response conflict^{14–16,42}, this result strongly suggests that momentary lapses in attention adversely affect the ability to minimize

distraction from irrelevant stimuli. It also bolsters our view that momentary lapses in attention reduce the quality of behaviorally relevant perceptual representations, as reducing the quality of such representations is known to allow distracters to exert a stronger influence on behavioral performance³⁰.

Sixth, we found that greater right TPJ activity and greater right IFG activity in the current trial were both associated with faster response time in the next trial, but not in the current trial. Because these regions have been implicated in stimulus-triggered reorienting of attention^{18,43}, our findings suggest that, during a brief attentional lapse, the abrupt onset of a new stimulus results in the reorienting of spatial attention back to the location at which behaviorally relevant stimuli are being presented, which facilitates performance in the next trial. This interpretation fits with the view that the right IFG participates in stimulus-triggered attention in numerous contexts, including reorienting attention¹⁸ and response inhibition⁴³. Moreover, it extends the roles of the right TPJ and the right IFG in stimulus-triggered reorienting of attention to include recovering from brief attentional lapses.

Of importance, our findings cannot easily be explained by other factors, besides attentional lapses, that contribute to response time variability. For instance, stimulus repetition is associated with positive relationships between faster response times and reduced sensory cortical activity⁴⁴, rather than the negative relationships we observed. Variability in motivation also modulates brain-behavior relationships, but often through the well-known influence of reward circuitry on attentional systems⁴⁵. Thus, there is little support for purely nonattentional interpretations of our data.

In conclusion, our findings provide a new, system-wide view of the neural bases of momentary lapses in attention, which reveals how such lapses impair goal-directed behavior. More broadly, our results illustrate that important questions about the neural substrates of behavior can be addressed by investigating trial-by-trial relationships between response time and brain activity. Future studies using similar approaches may therefore reveal a wide variety of interesting brain-behavior relationships whose location and nature may vary in theoretically important ways with the task under investigation.

METHODS

Participants. Sixteen healthy participants (9 male, 7 female, age range 18–35) took part in the study. All had normal or corrected-to-normal vision with no history of serious neurological trauma or disorders. All except one were right-handed. Participants gave informed written consent before the experiment in accordance with the Duke Medical Center Institutional Review Board for human subjects. Before the fMRI session, each participant practiced one or two blocks of the experimental task. Participants were paid \$20 per hour for their participation, which lasted approximately 2 h.

Task. For the duration of each run, participants identified either the large, global letter ($3.3^\circ \times 2.1^\circ$) or the small, local letters ($0.6^\circ \times 0.4^\circ$) of a hierarchical stimulus that appeared centrally for 200 ms at the beginning of each 2.5-s-long trial (Fig. 1). A red fixation dot was displayed at the center of the screen throughout each run, and the experimental stimuli appeared briefly at locations surrounding the dot. Each run contained 48 congruent stimuli (a global H made of local Hs or a global S made of local Ss) and 48 incongruent stimuli (a global H made of local Ss or a global S made of local Hs). Participants were asked to press one button if the target letter was an H and a different button if the target letter was an S, using the index and middle fingers of their right hand. Participants performed three runs of the global task and three runs of the local task.

In each run, congruent and incongruent trials were presented in a counter-balanced order such that each trial type was preceded equally often by every trial type in the design. The intertrial interval (ITI) ranged from 0 to 5 TRs, following a roughly exponential distribution that favored short ITIs. Such

jittering of the ITI increases the efficiency with which response estimates for distinct trial types are made when brain responses to different stimuli overlap⁴⁶ and is therefore highly advantageous when estimating stimulus-locked fMRI activity in a multiple regression framework^{23,47}.

Data acquisition. A PC was used to present stimuli and to record participants' responses. Visual stimuli were projected onto a screen at the back of the magnet's bore that participants viewed through a mirror. Button-press responses on an fMRI-compatible response box were made using the index and middle fingers of the right hand.

Structural images for each participant were collected using a T1-weighted spin echo sequence on a 1.5-Tesla GE whole-body scanner (TR = 500 ms, TE = 14 ms, flip angle = 90°, 17 contiguous 7.5-mm-thick slices with in-plane resolution = 0.94 mm × 0.94 mm). Functional images, which measured the blood oxygenation level-dependent (BOLD) signal, were collected using a spiral imaging sequence (TR = 1.25 s, TE = 40 ms, flip angle = 90°, 17 contiguous 7.5-mm-thick slices with in-plane resolution = 3.75 mm × 3.75 mm). Each participant completed six runs of the experimental task. During each run, 296 brain volumes were collected. The first six functional images of each run contained no trials and were discarded.

Data analysis. SPM'99 (ref. 48) was used to correct the functional images for head motion, normalize these images to standard space and spatially smooth them with a three-dimensional Gaussian filter (full-width at half-maximum, FWHM, = 8 mm). The time series for each functional run was analyzed using customized software, which implements a version of the general linear model that makes no assumptions about the shape of the BOLD response. This linear regression approach, sometimes called the finite impulse response (FIR) model, estimates the average stimulus-locked fMRI response associated with each trial type and has been validated in numerous previous studies^{17,23,31}. The linear model included 12 regressors to model the average stimulus-locked fMRI response for each trial type. These 12 regressors corresponded to 12 time points of the average fMRI response evoked by each trial type, which we assumed lasted 15 s (that is, 12 TRs).

RT regressors. We also included 12 additional regressors for each trial type to probe whether and how the magnitude of the fMRI response in each trial varied with RT. These parametric regressors⁴⁹, which we refer to as RT regressors, modeled trial-to-trial variance in the average fMRI signal for a trial type that varied linearly with trial-to-trial variance in correct RTs for that trial type. Relative RT for each trial was measured as the mean-subtracted RT score, as follows: RT for that trial (in seconds) minus the mean RT for correct trials of that trial type in that functional run. Within the linear model, each time a trial type was presented and a correct response was made, we included not only 12 regressors of unit value (that is, 1), which corresponded to each time point of the average fMRI response, but also 12 RT regressors with a value of the mean-subtracted RT for that trial. Each RT regressor modeled the effect of RT on fMRI activity at one time point of the relevant trial type's average fMRI response.

Because the average of any distribution from which the mean is subtracted is zero, the regressors that coded the RT regressors for any given trial type were orthogonal, on a time point-by-time point basis, to the regressors that coded for the average fMRI response for that trial type (that is, the dot product of two corresponding columns in the linear model was zero). Thus, each set of 12 RT regressors modeled the degree to which an individual trial's fMRI response varied with response time without changing the estimate of that trial type's average fMRI response. Trials with an omitted or incorrect response (on average, 3.28% of trials) were coded with separate regressors (without RT regressors), so that only correct response times would contribute to the parameter estimates for the RT regressors. Finally, the linear model for each run included six regressors for head motion (that is, SPM'99 motion estimates) and two separate regressors for the linear trend and *y*-intercept terms.

Frontal control regions. Because we were interested in prestimulus activity in frontal control regions, our analyses in these regions were implemented using a second regression model for each participant. Here, we modeled 18 time points of the average fMRI response associated with each trial type, which included 6 prestimulus points and 12 poststimulus points (that is, we modeled from 7.5 s

before stimulus onset to 15 s after stimulus onset). We also included 18 RT regressors for each trial type, one for each time point of its average fMRI response.

Ventral fronto-parietal regions. To investigate whether right TPJ activity and right IFG activity are associated with ending momentary lapses in attention, we estimated a third regression model for each participant. In this model, the 12 regressors that coded for each trial type's average fMRI response were still time-locked to the onset of the current trial. However, the values of the RT regressors were derived from the RT that occurred in the trial immediately following the current trial, rather than from the current trial itself. Therefore, this regression analysis determined whether trial-to-trial variability in fMRI activity for the current trial could be accounted for by trial-to-trial variability in RT for the next trial. To ensure that only correct trials contributed to this analysis, RT regressors for an individual trial were coded only when the responses made in both the current trial and the next trial were correct.

Units of estimated fMRI responses. Following the estimation of a particular regression model, the parameter estimates from each run were converted to units of percent change from a session-specific fixation baseline (that is, the *y*-intercept term for that run) and then averaged across runs for each participant separately. The parameter estimates for the RT regressors were expressed in units of percent change in fMRI signal per second of increased RT above the mean RT.

ROI analyses. Unless otherwise noted in the Results section, ROIs were functionally defined using a voxelwise, random-effects, one-way, repeated-measures ANOVA on the average fMRI response to all target stimuli (12 time points). The resulting *F*-map was thresholded somewhat conservatively ($F_{11,165} = 3.7$, $P < 0.0001$, 5 contiguous voxels), but at a level that still allowed us to identify large numbers of activated voxels throughout the brain.

Each ROI was a 27-voxel cube centered on a local maximum in a statistical map. Parameter estimates for individual trial types were averaged across all voxels within each ROI. The results of ROI analyses on the RT regressors were unbiased because they were orthogonal to the contrasts that were used to create the ROIs (for example, the average fMRI response for all target stimuli versus baseline). Therefore, $P < 0.05$ (one-tailed) was considered to be significant. All statistical tests in the present study were conducted using random-effects analyses so that our conclusions would generalize to the population. Conversion from MNI to Talairach⁵⁰ coordinates was implemented with two non-linear transformations (<http://www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispace.shtml>).

ACKNOWLEDGMENTS

This research was supported by a postdoctoral National Research Service Award to D.H.W. (1 F32 NS41867-01) and by US National Institute of Health grants to M.G.W. (MH60415 and P01 NS41328, Project 2).

COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

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