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REVIEW

**Recent theoretical, neural, and clinical advances in sustained attention research**Francesca C. Fortenbaugh,<sup>1,2,3,4</sup> Joseph DeGutis,<sup>2,3,4</sup> and Michael Esterman<sup>1,2,3,5</sup>

<sup>1</sup>Neuroimaging Research for Veterans (NeRVe) Center, VA Boston Healthcare System, Boston, Massachusetts. <sup>2</sup>Boston Attention & Learning Laboratory, VA Boston Healthcare System, Boston, Massachusetts. <sup>3</sup>Geriatric Research, Education, & Clinical Center (GRECC), VA Boston Healthcare System, Boston, Massachusetts. <sup>4</sup>Department of Psychiatry, Harvard Medical School, Boston, Massachusetts. <sup>5</sup>Department of Psychiatry, Boston University School of Medicine, Boston, Massachusetts

Address for correspondence: Michael Esterman, Ph.D., 150 S. Huntington Avenue, Boston, MA 02130. [esterman@bu.edu](mailto:esterman@bu.edu)

Models of attention often distinguish among attention subtypes, with classic models separating orienting, switching, and sustaining functions. Compared with other forms of attention, the neurophysiological basis of sustaining attention has received far less notice, yet it is known that momentary failures of sustained attention can have far-ranging negative effects in healthy individuals, and lasting sustained attention deficits are pervasive in clinical populations. In recent years, however, there has been increased interest in characterizing moment-to-moment fluctuations in sustained attention, in addition to the overall vigilance decrement, and understanding how these neurocognitive systems change over the life span and across various clinical populations. The use of novel neuroimaging paradigms and statistical approaches has allowed for better characterization of the neural networks supporting sustained attention and has highlighted dynamic interactions within and across multiple distributed networks that predict behavioral performance. These advances have also provided potential biomarkers to identify individuals with sustained attention deficits. These findings have led to new theoretical models explaining why sustaining focused attention is a challenge for individuals and form the basis for the next generation of sustained attention research, which seeks to accurately diagnose and develop theoretically driven treatments for sustained attention deficits that affect a variety of clinical populations.

**Keywords:** sustained attention; vigilance; mind wandering; reward; attention networks; default mode network

The ability to sustain focused attention over prolonged periods of time has long been of interest to cognitive psychologists. From detecting infrequent targets on a radar screen to driving, sustained attention is a foundational cognitive function that underlies other cognitive domains, such as learning and memory. This review seeks to highlight recent findings in cognitive neuroscience over the last 5 years that have built on the findings from previous decades (e.g., starting with Mackworth<sup>1</sup> in the 1950s), increasing our theoretical understanding of the cognitive and neural mechanisms involved in sustaining attention. The present review also seeks to bridge findings in disparate areas of behavioral, neuroimaging, and patient-oriented research, providing a framework for both those who study attention as it is most broadly defined and those

whose research focuses on sustained attention or vigilance. There are four main questions that the present review focuses on. Why is it challenging for individuals to maintain focused attention on a task for extended periods of time? How does focused attention fluctuate over time and what factors modulate these fluctuations? What are the neural networks that support sustaining attention, and how are these networks related to fluctuations in sustained attention? What is known about sustained attention deficits in clinical populations, and how does this knowledge inform our understanding of sustained attention mechanisms and the development of novel rehabilitation approaches? Of note, the present review focuses on research published within the last 5 years. Several important reviews of the sustained attention

literature have been published reviewing earlier findings.<sup>2–4</sup>

## Models of sustained attention

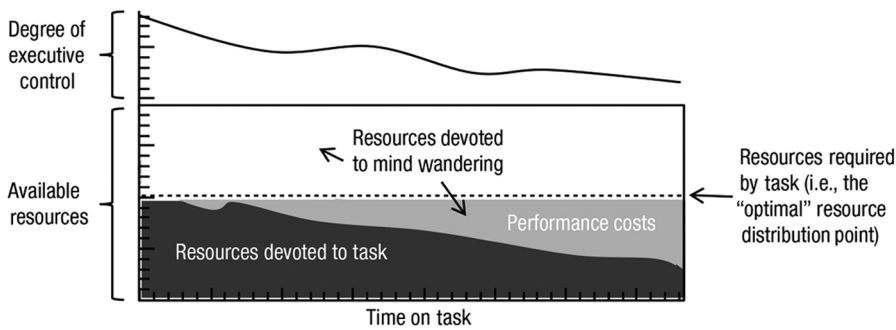
We first consider how sustained attention is conceptualized. Most broadly, sustained attention is differentiated from other classes of attention by the duration of the required activity. That is, sustained attention requires an observer to maintain engagement in a specific task (e.g., detecting a rare target) over an extended period of time. While some researchers impose a lower limit on how long attention must be focused on a specific goal for a task to be considered as measuring sustained attention, such as the 10-s limit for studies included in the meta-analysis of vigilant attention by Langer and Eickhoff,<sup>3</sup> such cutoffs reflect operational definitions, and currently there is no consensus that sustaining attention evolves into some unique attentional mechanism after a specific duration. This highlights some of the difficulty that arises in delineating what aspects of attention a task measures and why the term “sustained attention” is broadly used across studies. In this review, we will mainly focus on classic types of paradigms for measuring sustained attention (e.g., rare target vigilance tasks, continuous performance tasks (CPTs)), though we will also highlight how other nontraditional paradigms can inform models of sustained attention.

At the broadest level, attempts have been made to delineate subtypes of attention. In an early review of the neural bases of attention, Posner and Peterson<sup>5</sup> defined three subsystems of attention: (1) orienting to sensory events, (2) detection of signals for focal and conscious processing, and (3) alerting, which includes both tonic (over longer time intervals) and phasic (for brief periods < 1 s). More recent evaluations of these systems have replaced the detection system with the executive attention system, which still includes the initiation of focal attention at target detection but now also includes other functions, such as monitoring and conflict resolution.<sup>6,7</sup> Importantly, as noted by Tang *et al.*,<sup>8</sup> sustained attention is not necessarily synonymous with the alerting system in this three-system model,<sup>6,9,10</sup> but may include aspects of both tonic alerting and orienting.

A recent cognitive-based taxonomy developed by Chun *et al.*<sup>11</sup> dissociates attention subtypes based on whether the target of attentional focus for selection

and modulation is external or internal, with external referring to perceptual/sensory stimuli and internal referring to the selection of executive/cognitive control processes, including task rules, response execution, and decisions. Under this taxonomy, sustained attention is not considered a separate system but rather the “challenge of maintaining attentional focus,” whether external or internal, over extended periods of time. While this model (and others) suggests that sustained attention ( $A$ ) for time ( $T$ ) is not just  $A \times T$ , it remains unspecified. Although this conceptualization of sustained attention does not describe the underlying neural mechanisms that support vigilance over time, the model highlights one of the fundamental behavioral characteristics that has been used to measure sustained attention: the vigilance decrement or decrease in performance over time.

Besides debates about where sustained attention fits into the overall taxonomy of cognition, there is also debate about the source of one of the most fundamental aspects of sustained attention—vigilance decrements. The two dominant theories about this phenomenon over the last few decades include (1) the resource-depletion (overload) account, which assumes that attentional resources decline with time and thus reduce the amount of attention that can be focused on the task at hand,<sup>12–16</sup> and (2) the mindlessness (underload) account wherein repetitive and/or monotonous responses to targets are understimulating and lead to disengagement from the task and observed performance deficits.<sup>17–21</sup> Investigations into these models continue to be active areas of research, including studies examining how manipulating target salience mediates mind wandering and error rates<sup>22–24</sup> and how dual tasks<sup>25</sup> or interrupting performance with alternative tasks<sup>26</sup> affects performance. The results of recent studies have produced findings that are difficult for either theory to fully explain. As noted by Thompson *et al.*,<sup>27</sup> findings that increasing task engagement can improve performance on some tasks despite increasing task demands<sup>28,29</sup> and that self-reported mind wandering increases with time on task<sup>21,30</sup> are inconsistent with the resource-depletion account. In contrast, pure mind-wandering accounts have difficulty accounting for reports<sup>12,16</sup> that vigilance tasks are stressful/effortful and that factors that increase attention to the task (e.g., displaying pleasant stimuli) either



**Figure 1.** Resource-control model of sustained attention. Schematic illustration of the mechanisms proposed to lead to vigilance decrements over time. This figure shows that the total amount of attentional resources available to an observer remains constant over time, as does the amount of resources needed for the primary task (dotted line), while the degree of executive control declines (y-axis). This results in a disproportionate amount of resources being devoted to mind wandering (the combination of the white and light gray portions) and not enough resources being devoted to the primary task (the dark gray portion), resulting in performance costs (the light gray portion beneath the dotted line). Adapted with permission from Ref 27.

have no effect on or decrease sustained attention performance.<sup>197</sup>

In the last 5 years, two novel models have been proposed that may better account for vigilance decrements and behavioral findings related to task difficulty/engagement. This includes the opportunity-cost model,<sup>31</sup> which proposes that the degree of cognitive resources that can be deployed at any given time is limited but does not wane over time. However, the selection of a specific task reflects a cost in that only a limited number of tasks can be completed at the same time, and the subjective value of maintaining one cognitive operation over another tends to increase over time, leading to the perception of increased effort. The focus in this theory is thus how cognitive effort is distributed on the basis of reward, valuation, and/or motivation, not diminishing availability. While the opportunity-cost model can account for many findings in the sustained attention literature, we note that this is a general model of cognitive control and was not designed to specifically address sustained attention.

In contrast, the resource-control<sup>27</sup> theory was developed to specifically account for sustained attention. The resource-control theory developed from findings suggesting that mind wandering (self-generated thought) is the default state for individuals<sup>32</sup> and proposes there is a continuous bias for attentional resources to be directed toward mind wandering. This is in line with the external–internal dichotomy of voluntary attention developed by Chun *et al.*<sup>11</sup> and current views of mind wandering,<sup>21</sup> in which attention can be divided

between or focused on external task goals and internally generated thoughts. This model accounts for vigilance decrements by proposing that, while attentional resources do not decrease over time, with time on task, executive control of attention toward task goals fails as more and more attentional resources are devoted toward mind wandering (Fig. 1). While the resource-control theory was developed to account for behavioral findings on sustained attention tasks given the interplay between attentional focus and mind wandering over time, this model predicts that regions associated with the executive attention network and default network regions should both fluctuate in time with fluctuations in sustained attention performance and that they should be inversely related.

Additionally, though the resource-control theory proposes a competitive relationship between task-related focal attention and mind wandering, the shift of the control function from attentional systems to a broader executive control system implies that failures of sustained attention can occur in multiple ways. In particular, while there may be a pull toward greater mind wandering over time (internal focus of attention),<sup>21,30</sup> such control failures originating from a separate executive control system could also lead to attentional resources being shifted toward external distractors (e.g., sensory experiences related to the environment or sensations of physical discomfort).

Finally, both the opportunity-cost and resource-control theories suggest that the degree of intrinsic motivation, and thus the ability to exert effort,

will wane over time. However, by manipulating the potential costs/rewards associated with staying on task, it should be possible to directly affect time-on-task decrements. Such manipulations have recently been studied using reward paradigms. Common motivation/reward paradigms use incremental or trial-based, performance-based gains/losses, and, as such, the overall value of the task decreases with time on task. This may explain why, for example, Esterman *et al.*<sup>33</sup> found that these typical reward manipulations increased overall performance (i.e., higher accuracy and lower response variability), while vigilance decrements in performance over time were unaffected. In order to keep overall task value constant, another study<sup>29</sup> was completed where participants had the opportunity to gain a significant reward of \$18 if they correctly withheld response to a specific target mountain scene. Results here showed that the typical vigilance decrement found in the previous study could be eliminated when the anticipated large reward was withheld until the end of the 10-min run. The fact that changing the opportunity-cost structure of the reward manipulation could eliminate the vigilance decrement is better accounted for by the opportunity-cost and resource-control theories than pure resource (overload) theories and suggests that the perceived value of maintaining high levels of performance on sustained attention tasks can alter not only the overall performance of participants but also changes in their performance over time.

Additional pupillometry studies have also provided neurophysiological support for motivation and reward modulating sustained attention and vigilance decrements. Pupil diameter is known to increase in response to salient stimuli and increasing task demands. The degree of dilation has been shown to correlate with task engagement and is thought to be at least partially driven by norepinephrine released by the locus coeruleus (LC).<sup>34–36</sup> This provides an important approach to studying sustained attention given that the LC is located in the pons and not easily measurable in neuroimaging studies. The LC has long been thought to play an important role in sustained attention by modulating thalamic and cortical activity, as reviewed by Sarter.<sup>2</sup> Hopstaken *et al.*<sup>34</sup> had participants perform a 2-h version of a two-back working memory task and observed decreases in task performance, self-reported attention to task, and

stimulus-evoked pupil dilation. However, after 2 h of task, participants were informed that the remaining duration of the experiment would depend on their performance, with better performance reducing the remaining time. Consequently, task accuracy increased, as did stimulus-induced pupil dilation, back to levels seen in the initial task blocks. Another study<sup>37</sup> used a performance-based monetary reward manipulation of a traditional psychomotor vigilance task and included a secondary delayed-discounting task. Results here showed that participants increasingly discounted the value of the future monetary rewards as the task duration increased, consistent with the effort required to maintain sustained attention being seen as a cost against which the perceived gain of monetary reward was calculated. Additionally, prestimulus pupil diameter was larger across the entire block of trials in the reward conditions compared with baseline, and not just during stimulus presentation, consistent with increased attentional effort in higher-reward conditions with improved task performance.

Finally, while experience sampling or thought probes have often accompanied sustained attention tasks, like the sustained attention to response task (SART),<sup>21,38</sup> recently paradigms have shown a distinction between task-unrelated thoughts (TUTs) that are intentional versus unintentional, such that intentional TUTs are more related to lack of motivation and greater vigilance decrements.<sup>39,40</sup> Collectively, these studies are inconsistent with resource or mindlessness theories alone and fit with the newer models that take into account motivation and valuation of attentional allocation.

### Recent developments in paradigms to investigate sustained attention

In addition to the above-mentioned theoretical developments, there have also been notable changes in the paradigms used to study sustained attention. Classic vigilance tasks have involved detection or discrimination of infrequent targets over minutes to hours.<sup>1,41,42</sup> Variants of these paradigms are currently used by human factors researchers (e.g., studying train operation) and have also been used to study the effects of sleep deprivation (e.g., psychomotor vigilance task<sup>43–46</sup>). CPT paradigms, developed for assessing sustained attention over a shorter period of time, sometimes reverse the



**Figure 2.** Gradual-onset continuous performance task (gradCPT). Schematic illustrating the gradual transition from a nontarget city image to a target mountain image. Images show the first image transitioning to the second at 100%, 75%, 50%, 25%, and 0% image coherence. Participants are required to press a button each time a city scene is presented (90% of trials) and withhold responses when infrequent mountain scenes are presented on the remaining 10% of trials. In the standard paradigm, one image transitions in from the previous image over 800 milliseconds.

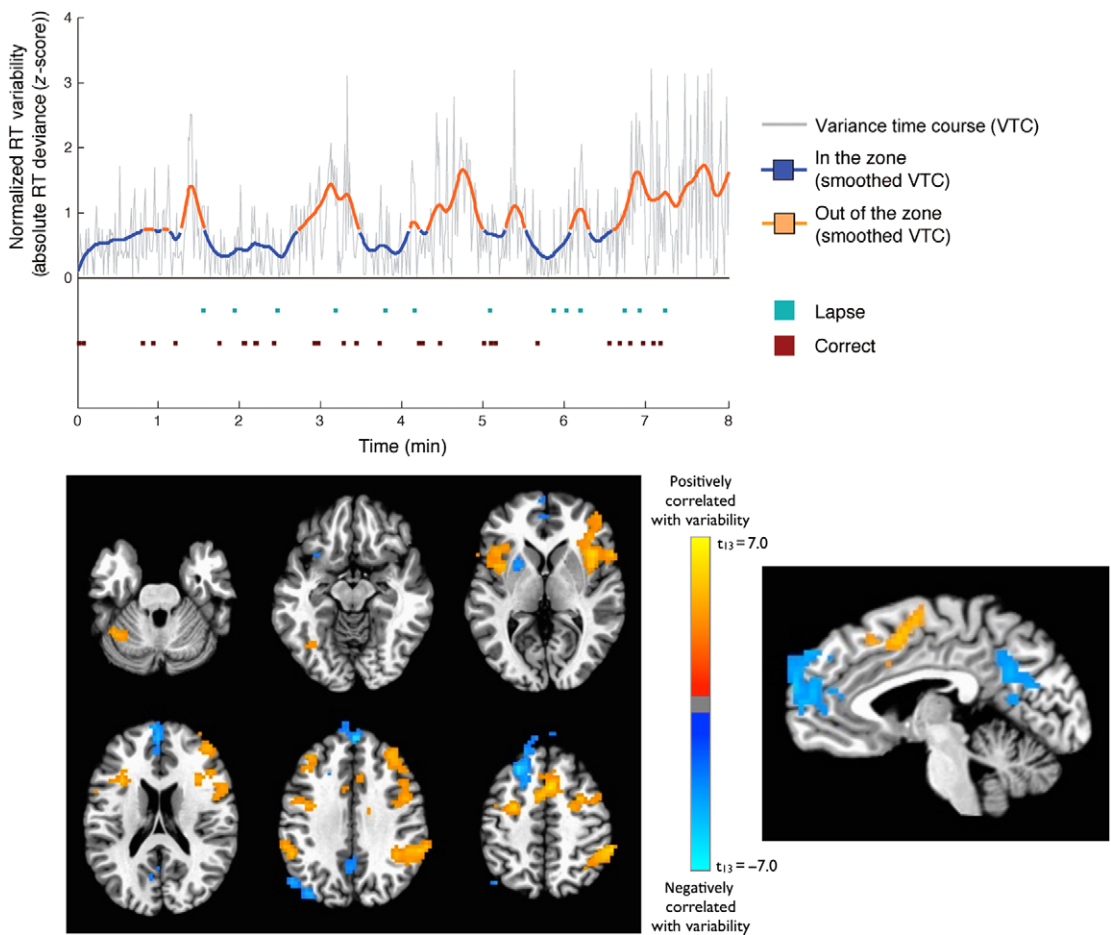
frequency of target and nontarget stimuli, with responses required to frequent nontarget stimuli (i.e., not-X CPT tasks). Though numerous variations of these CPTs have been developed, two of the most popular are Conner's CPT,<sup>47</sup> which is often used to assess attention deficit hyperactivity disorder (ADHD), and the SART,<sup>19,48</sup> initially developed to assess patients with acquired brain injury and healthy populations. One benefit of these go/no-go task variations that has been more recently appreciated is that frequent responses are collected, allowing more fine-grained analyses of response-time fluctuations, in addition to detection/discrimination accuracy. Validating this as a measure of moment-to-moment attention, studies have connected fluctuations in reaction time with increased levels of mind wandering.<sup>49</sup> It is important to note that questions have been raised regarding the extent to which tasks like the SART tax sustained attention versus response inhibition.<sup>50</sup> These alternative perspectives of the not-X CPT tasks concern the degree to which strategic factors, such as speed–accuracy trade-offs, are reflected in performance in addition to sustained attention ability.<sup>50,198–200</sup> However, others have suggested that both X and not-X CPT tasks measure overlapping attentional constructs,<sup>24,54,201</sup> and recent findings that have shown relationships between performance on the SART and measures of real-world deficits in sustained attention<sup>51</sup> help to alleviate some of these concerns. We note, however, that this continues to be an active area of debate in the literature.

Building on these paradigms, Esterman *et al.*<sup>52</sup> developed a novel go/no-go CPT called the gradual-onset continuous performance task (gradCPT). The main innovation of this paradigm is the gradual fading of one stimulus image into the next, remov-

ing the abrupt onsets and offsets of images and thus exogenous cues that signal trial-to-trial stimulus changes (Fig. 2). With the frequent responses to nontarget stimuli, Esterman *et al.*<sup>52,53</sup> defined the *variance time course* (VTC): a trial-by-trial measure of reaction time variability (Fig. 3A). Using a median split of trials in the VTC, they further defined periods of being “in the zone” characterized by low reaction time deviations from the mean and periods of being “out of the zone” characterized by high deviations from the mean (very fast or slow reaction times), and demonstrated that out of the zone periods are associated with reduced accuracy in target discrimination relative to in the zone periods.<sup>52,54</sup> Estimates of overall response variability and its relationship to task performance have long been of interest to researchers studying healthy individuals<sup>55</sup> and clinical populations<sup>43,56</sup> on sustained attention tasks. However, response variability is typically assessed as an interindividual difference measure using the standard deviation or coefficient of variation of all trials. The development of the VTC therefore provides a novel measure that can be applied to multiple tasks;<sup>57,58</sup> a time series that allows for moment-to-moment assessments of response stability on any given trial.

Recently, several other paradigms<sup>59</sup> have been utilized to test a broader range of experimental questions regarding attention fluctuations. These include tapping tasks that require participants to maintain a steady rhythm of finger taps over several minutes.<sup>57</sup> This task does not include stimulus discrimination/detection, and no accuracy measure is derived. Instead, this task allows for estimations of reaction time fluctuations in the absence of external stimuli such that all responses are internally generated. This provides an important experimental



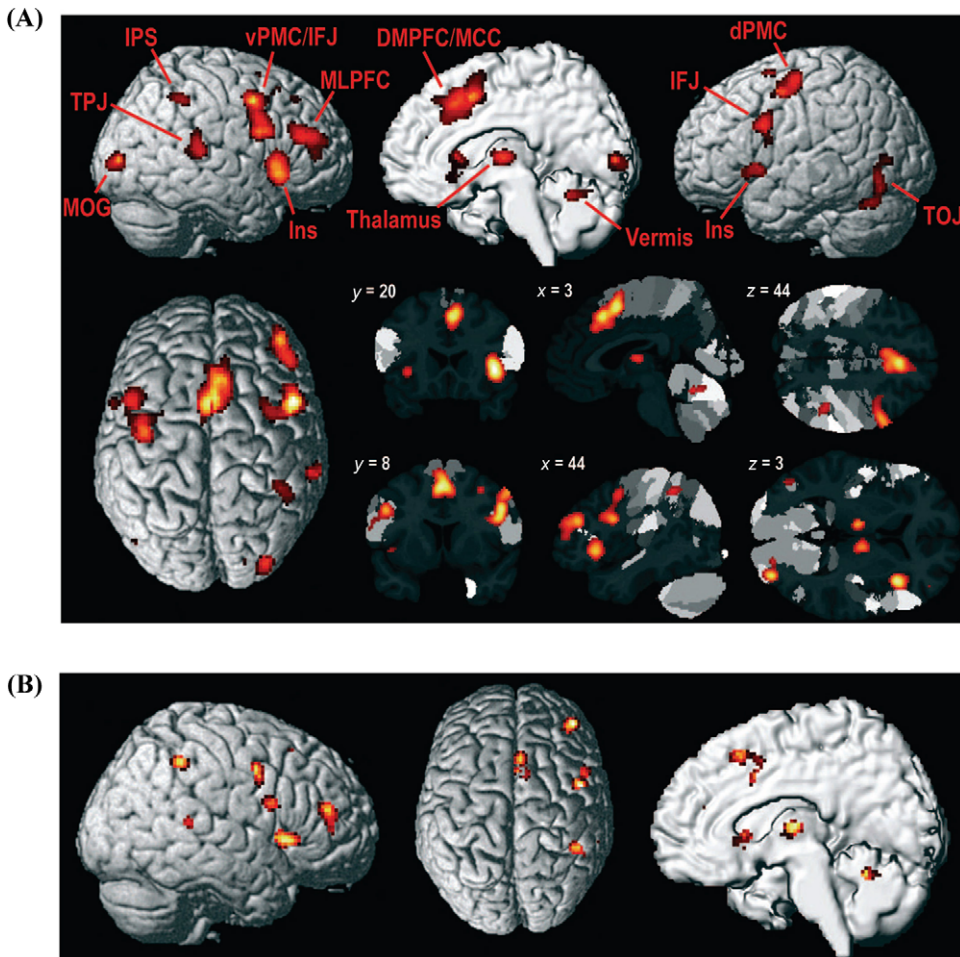


**Figure 3.** The variance time course (VTC) from the gradCPT. The top panel shows an example VTC for a single, representative participant over the 8-min task block. The smoothed VTC used in regression analyses is highlighted in blue for the periods when the participant was in the zone and orange for when the participant was out of the zone. The bottom panel shows the VTC–BOLD signal correlation. Regions in blue are negatively correlated with the VTC (i.e., they are associated with relative stability of reaction time (lower variability)). Regions in orange are positively correlated with the VTC and associated with relative instability of reaction times (higher variability). The bottom panel is adapted with permission from Ref. 72.

variation that allows for tests of the extent to which fluctuations in reaction time variability, which are used as behavioral measures of attentional stability, are stimulus independent. Additionally, novel variants of CPTs have been developed, such as the continuous temporal expectancy task, which includes flickering stimuli that allow for estimations of evoked cortical responses using electroencephalography.<sup>60</sup> Additionally, novel visual search<sup>61</sup> and working memory<sup>62,63</sup> tasks have been used to specifically explore the role of sustained attention lapses and motivation in performance fluctuations.

**Neural networks involved in sustaining attention**

The last few years have seen an increased interest not only in characterizing task-evoked regional activity but also in understanding how such regions fit within large-scale neural networks that are involved in supporting diverse aspects of cognition. While the specific networks and the labels applied to networks can shift depending on the study, recent work has pointed to several important transformations in our understanding of the neural basis of sustained attention. The following section will outline some of



**Figure 4.** The “vigilant attention” network. (A) Results from the meta-analysis of 67 fMRI studies by Langner and Eickhoff<sup>3</sup> overlaid on the template brain with maps of cytoarchitectonically defined areas as included in the SPM Anatomy Toolbox. Coordinates refer to the Montreal Neurological Institute space and follow the neurological convention (left = left). (B) Foci of brain activity that show significantly stronger across-experiment convergence with increasing duration of vigilant attention task. DMPFC, dorsomedial prefrontal cortex (including presupplementary motor area); dPMC/vPMC, dorsal/ventral premotor cortex; IFJ, inferior frontal junction; Ins, anterior insula; IPS, intraparietal sulcus (including adjacent inferior parietal lobule); MLPFC, midlateral prefrontal cortex; MOG, middle occipital gyrus; TOJ/TPJ, temporo-occipital/temporoparietal junction. Figure is adapted with permission from Ref. 3.

these major contributions, including (1) sustained attention supported by distributed neural networks; (2) the default mode network, which was previously thought of as a task-negative<sup>64</sup> or task-irrelevant<sup>65</sup> network, but has recently been reconceived as a network that plays a more complex role in supporting sustained attention, specifically, and cognition generally; and (3) novel paradigms and analyses that have allowed us to assess the neural mechanisms underlying sustained attention at a finer temporal scale, assessing moment-to-moment fluctuations in

attentional stability, corresponding changes in neural dynamics, and the impact of reward and task engagement on these dynamic relationships.

#### *Evoked activations and the vigilance network*

In their meta-analysis of 67 functional magnetic resonance imaging (fMRI) studies on vigilant attention (Fig. 4A), Langner and Eickhoff<sup>3</sup> identified 14 clusters that were consistently activated across various sustained attention tasks. These included (1) the bilateral presupplementary motor area (pre-SMA)

and the midcingulate cortex extending toward the anterior medial prefrontal cortex (mPFC); (2) the bilateral inferior PFC extending into the ventral premotor cortex (vPMC); (3) the bilateral anterior insula, including the right frontal operculum; (4) the bilateral thalamus; (5) the right midlateral PFC; (6) the right temporoparietal junction; (7) the right inferior parietal lobule and intraparietal sulcus; (8) the right middle occipital gyrus; (9) the left dorsal premotor cortex; (10) the left temporo-occipital junction; and (11) the cerebellar vermis. As seen in Figure 4A, this vigilant attention network spans several other attention-related networks identified with other attention paradigms, as well as task-positive networks that are not exclusively thought to be involved in attentional processes. For example, some overlap is seen with the dorsal and ventral attention networks identified by Corbetta *et al.*,<sup>66,67</sup> which are involved in the control of space-based and feature-based attention and reorienting to salient stimuli outside the focus of attention, respectively. The regions also correspond to part of the executive control attention networks identified by Posner *et al.*,<sup>5,6,68</sup> including partial overlap with the frontoparietal control system and the cingulo-operculum system, also referred to as the salience network.<sup>69</sup> Of note, Langner and Eickoff<sup>3</sup> also conducted an across-study examination of time-on-task effects (Fig. 4B). That is, which areas within the vigilant attention network were more likely to show task-related activity in studies with longer task durations? This analysis showed positive correlations in right hemisphere regions, predominantly in the frontoparietal and salience networks. Importantly, however, the analysis does not directly test which regions are associated with vigilance decrements and changes in behavioral performance within individual participants.

Within the last 5 years, however, studies have begun to look more at intraindividual effects of time on task and moment-to-moment fluctuations. For example, Hilti *et al.*<sup>70</sup> examined which regions are associated with changes in reaction time in individuals with small and large vigilance decrements. Examination of which regions correlated with trial-by-trial reaction time fluctuations revealed a bilateral fronto-cingulate-insular-parietal network that showed increased activity with slower reaction times (i.e., worse performance), including many of the areas identified in the across-study meta-analysis

of Langner and Eickoff.<sup>3</sup> Of note, when participants with low versus high reaction time slopes were compared (i.e., participants with small versus large vigilance decrements), only the pre-SMA was differentially correlated with reaction times to target stimuli, showing a stronger correlation with reaction times in the participants with small vigilance decrements. The regions identified in this study also overlap with the salience network identified in other studies, as well as the executive attention network.<sup>6</sup> The fact that the pre-SMA was more strongly coupled with reaction time in participants with smaller vigilance decrements suggests that this region may be critical for maintaining attentional focus on task-relevant goals, consistent with other studies of voluntary attention.<sup>71</sup> However, given that a traditional vigilance task was used, only 12 target trials requiring an overt response occurred during a given run, limiting the number of observations used in the data analyses.

While Hilti *et al.*<sup>70</sup> identified task-positive networks that track faster and slower reaction times, other studies have examined moment-to-moment fluctuations in reaction time variability. Using the gradCPT task, Esterman *et al.*<sup>52,72</sup> examined regions that either positively or negatively correlate with moment-to-moment fluctuations in response variability or VTC (see above). Results of these studies show that not only do task-positive regions, such as the pre-SMA, track changes in response variability, but the core default regions (anterior mPFC and PCC) also track these changes (Fig. 3B). In contrast to regions in the salience network, however, increases in blood oxygen level-dependent (BOLD) activity within these default regions are associated with decreases in response variability. Thus, when participants are in the zone and performing well on the task, default regions are relatively more active, while task-positive regions are relatively less active. In contrast, when participants are out of the zone and struggling to maintain performance levels on the task, task-positive regions are engaged to a greater extent, while activity in the core default network is suppressed. These results have been replicated across multiple studies and tasks.<sup>57,73,74</sup> Additionally, comparisons of trial-by-trial reaction times (as opposed to VTC) in the gradCPT<sup>52</sup> showed similar positive correlations to those observed by Hilti *et al.*,<sup>70</sup> particularly in several regions falling within the salience network, and no negative correlations,

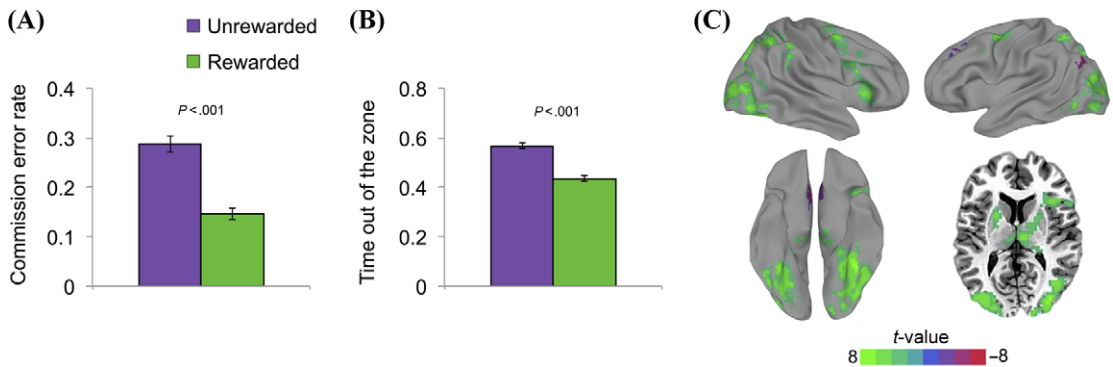


providing evidence that reaction time speed and reaction time stability are distinguishable.

These recent findings have begun to reveal a new perspective on the relationship between default mode and task-positive activity with attention. Specifically, the above studies<sup>52,57,72,74,75</sup> show that higher default mode activity is associated with lower reaction time variability and faster reaction times. Conversely, higher task-positive activity in the salience and dorsal attention networks tracks greater reaction time variability and slower reaction times. At first glance, these findings seem to contradict other studies<sup>3,5,67</sup> that have identified the salience and dorsal attention networks as critical regions for supporting attentional processes and motivated behavior.<sup>75</sup> Additionally, neuroimaging studies have shown that being off task, including boredom, mind wandering, and internal mentation associated with mind wandering, is associated with increased default mode activity.<sup>76–82</sup> Moreover, increased reaction time variability has long been studied as a marker of inattention in individuals with ADHD<sup>83,84</sup> and is associated with less deactivation of default mode regions across individuals.<sup>85,86</sup> That is, default mode activity is positively correlated with overall reaction time variability. These findings have led to the default mode interference hypothesis of attentional deficits in ADHD, and attention lapses more broadly, which proposes that self-reported mind wandering and disorders of attention are associated with failures to effectively suppress activity within the core default mode regions.<sup>76,86</sup> Importantly, however, this association between reaction time variability and default mode activity has primarily been measured across individuals; thus, the relationship is between interindividual rather than intraindividual reaction time variability. The recent research findings outlined above pose a theoretical challenge to the notion that default mode activity, response variability, and mind wandering all vary along the same axis. Indeed, a recent study by Kucyi *et al.*<sup>74</sup> provided evidence that default mode activity tracks both mind wandering and attentional stability. Using a modified gradCPT task that included thought probes, this study showed that evoked activity in the 30 s before a thought probe was both positively correlated with a participant's self-reported mind wandering and negatively correlated with their reaction time variability. Importantly, these correlations were mea-

sured for each participant individually, and, using a mixed-effects analysis, the authors demonstrated that reaction time variability and off-task ratings provide independent, additive effects in predicting activity within default mode regions. This suggests that spontaneous default mode activity seen during tasks not only represents the degree to which participants are on/off task, but also includes information regarding their attention state. This study, the first to our knowledge to measure the relationship between attentional fluctuations, mind wandering, and default mode activity within participants, provides compelling evidence that activity within the default mode network contains information about multiple cognitive operations, which general patterns that emerge across individuals cannot fully capture. Thus, previous models of higher default mode activity indicating participants being off task or inattentive are not wrong, but rather incomplete.

On the other hand, another study that helped to clarify the seemingly contradictory roles of task-positive attention networks and fluctuations in performance (i.e., higher activity out of the zone) examined the effects of motivation on neural activity during a sustained attention. Using the gradCPT, Esterman *et al.*<sup>75</sup> found that, quantitatively, activity within the dorsal attention, ventral attention, and frontoparietal networks, as well as the basal ganglia, was more associated with motivated performance (Fig. 5). Qualitative differences in activation were also observed that interacted with moment-to-moment fluctuations. When rewarded, participants proactively engaged many of these regions in order to reduce attentional lapses and also maintained similarly high task-positive activity during both optimal (in the zone) and suboptimal periods (out of the zone) or fluctuations in performance. On the other hand, when unrewarded, the same participants only engaged task-positive regions to a comparable degree in response to making errors and during periods of suboptimal performance, as if in reaction to immediate task demands. Thus, not only does reward-based motivation improve sustained attention performance, it also significantly changes one's neurocognitive strategy in a manner more consistent with opportunity-cost and resource-control models than strict resource-depletion models. This dissociation is also in line with other models of motivation and cognitive



**Figure 5.** Reward and sustained attention. (A) Commission error (CE) rate during rewarded versus unrewarded blocks. (B) Time spent out of the zone during rewarded versus unrewarded blocks. When rewarded, participants had a significantly lower lapse/CE rate and spent less time out of the zone ( $P < 0.001$ ). Error bars represent standard error of the mean. (C) Overall sustained activation differences between rewarded and unrewarded blocks, when controlling for transient target-evoked activations. Figure is adapted with permission from Ref. 75.

control<sup>87</sup> and further implicates these task-positive brain regions as having a nuanced role in sustained attention, where reactive activation (out of the zone) may be a marker of suboptimal attention, while proactive activation (rewarded blocks) may be a marker of optimal attention.

The concept of being in versus out of the zone represents intraindividual fluctuations in attentional state and performance. Outside of the sustained attention literature, researchers have investigated a similar concept, termed flow, which refers to a subjective state wherein there exists a perceived fit between task demands and one's abilities, leading to a sense of effortlessness and, importantly, a strong sense of intrinsic reward in engaging in the task.<sup>88,89</sup> To study flow, recent studies have manipulated how rewarding a task is by manipulating task difficulty, including optimal levels of difficulty meant to induce a state of flow, which are compared to very easy or very difficult conditions. These studies<sup>90,91</sup> have shown that optimal levels of difficulty are associated with decreases in default mode activity, which the authors suggest reflects the decrease in self-referential processing that is associated with being in a state of flow, and increases in task-positive regions, including the prefrontal and insular cortices. These patterns stand in contrast to the results of being in the zone outlined above, although one area of overlap across these studies is the putamen, which is associated with both reward and being in the zone.<sup>75</sup> One potential explanation for the discrepancies comes

from the study of reward and sustained attention<sup>75</sup> discussed above, which indicates that there are potentially two ways to get into the zone—one is less effortful and/or more efficient, accomplished with less task-positive network activity but at the cost of lower accuracy when unrewarded. The other is more about sustaining effort continuously and proactively, as indexed by greater task-positive network activity when rewarded. While flow may be akin to a highly rewarded and proactive attentional state, typical in the zone performance on sustained attention tasks without reward manipulations are more likely to elicit the former approach. It is important to note, however, that the above studies<sup>90,91</sup> manipulate states of flow using explicit task difficulty, which is not dissociable from intrinsic performance variation, while studies<sup>52,57,74,75,90,91</sup> measuring in and out of the zone fluctuations look at intraindividual performance, where extrinsic task difficulty is constant, and thus fluctuations are intrinsically driven. It thus remains an interesting question for future research to determine the extent to which the concepts of being in the zone and in a state of flow overlap or represent distinct cognitive and neurophysiological states.

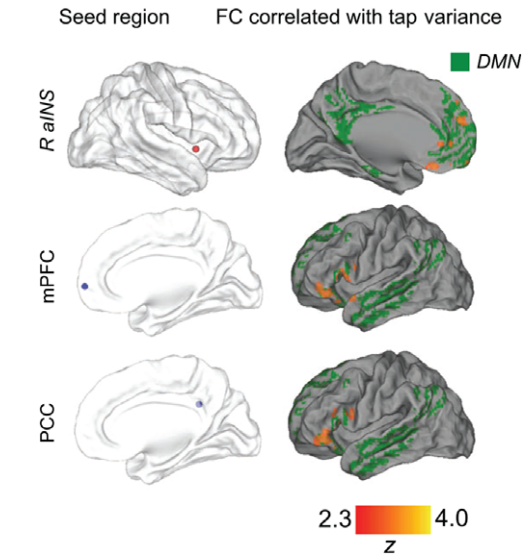
In sum, recent sustained attention studies suggest that important information can be obtained by examining multiple measures of behavior (e.g., reaction time variability, experience sampling), and that comparing activity both within and across networks and individuals is critical. Indeed, one recent study showed that, while the level of activity

in task-positive or task-negative regions does not differentiate performance, the relative activation between the two networks can predict the speed of responses on a psychomotor vigilance task.<sup>92</sup> The following section further explores these cross-network analyses comparing studies that utilize functional connectivity analyses.

### Functional connectivity analyses

Research on the neural networks involved in supporting cognition has increasingly focused on understanding how different networks interact with one another. In particular, resting-state fMRI functional connectivity analyses have been used to define intrinsic functional networks, with multiple parcels composed of varying complexity<sup>93–96</sup> and recent approaches incorporating anatomical and functional data to further guide segmentation.<sup>97,98</sup> Importantly, the utilization of functional connectivity approaches to studying sustained attention and cognition provides a complementary approach, as cognition does not simply arise from activity within a single region of the brain but rather evolves from the complex interplay within and across networks. The application of network-based functional connectivity analyses to the study of cognition has led to several theoretical advances. Perhaps most notable is the recognition that the default network is not just simply deactivated during the execution of cognitive tasks but plays a complex role in supporting cognition.<sup>64,99–101</sup>

This can be seen in a recent study by Kucyi *et al.*<sup>57</sup> that assessed attentional fluctuations using a finger-tapping task. While not a typical sustained attention task, moment-to-moment fluctuations in performance (and presumably sustained attention) were measured from the absolute variability in reaction times using the VTC method (see above). This study examined the temporal relationship between behavioral fluctuations in sustained attention and changes in functional connectivity, termed *dynamic connectivity*. Linking these fluctuations to sustained attention, the results of this study replicated the findings of Esterman *et al.*<sup>52</sup> with this experimental paradigm by demonstrating that increases in core default mode areas (mPFC and PCC) were associated with decreased tapping variability (i.e., being in the zone) while increased activity in the salience and dorsal attention networks was associated with increased tapping variability (i.e., being



**Figure 6.** Brain regions showing dynamic functional connectivity associated with ongoing fluctuations in tap variance. For each seed (left column), regions showing functional connectivity that positively correlated with tap variance are shown in red/yellow. These regions are overlaid on an independently defined map of the default mode network<sup>93</sup> in green to highlight that all significant clusters substantially overlapped with this network. Figure is adapted with permission from Ref. 57.

out of the zone). Extending these findings, the results of this study suggest important changes in functional connectivity within and across networks that track moment-to-moment changes in behavioral performance. Specifically, the results show that increases in response variability (i.e., being out of the zone) were associated with increased coupling (or decreased anticoupling) between the core default network nodes (mPFC and PCC) and the right anterior insula (salience network), as well as regions within the dorsomedial PFC, a part of the extended default network<sup>93</sup> (Fig. 6). There are two important implications from these findings. First, these results demonstrate that functional connectivity not only within but also across networks is not static and that temporal changes in functional connectivity may directly relate to task performance. The challenge of sustaining attention may not simply be in engaging one network or another, but how different networks are engaged with other networks. Second, these results highlight the evolving view of the default network, which may itself contain important subsystems, and the relative engagement of various regions may differ across tasks and time.<sup>57</sup>

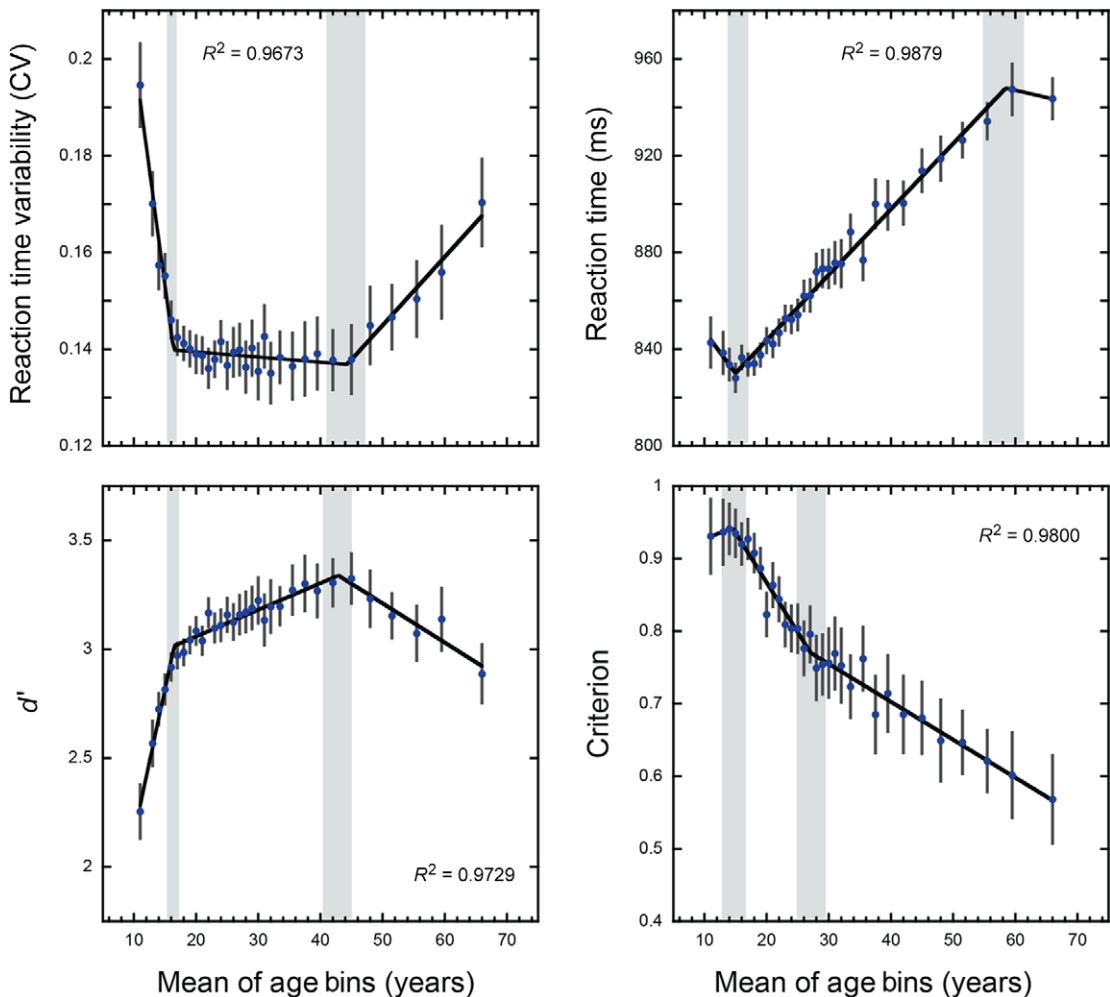
Beyond the default network, recent work has shown that activity in a range of areas outside attention networks can not only affect performance but can be used to predict individual differences in performance on sustained attention tasks. Using a 268-node whole-brain functional parcellation that included cortical, subcortical, and cerebellar regions, Rosenberg *et al.*<sup>102</sup> showed that it is possible to predict overall performance on the gradCPT task with functional connectivity patterns, both while participants completed the task and during a resting scan, suggesting that the pattern of connections derived from the functional scan are, at least in part, intrinsic connections and stable during rest. Additionally, using the connection patterns derived from healthy adults who completed the gradCPT task, the authors were able to predict ADHD severity scores in over 100 children using rest scans collected at a different site. The prediction ability of these connectomes further validates the importance of functional connectivity in supporting sustained attention ability. Interestingly, of all the connections defined in this network, less than half fall within traditional attention or vigilance networks. Other important nodes include cerebellar, subcortical, limbic, and occipital regions. These results again highlight that a vast network of regions, while not principal players in activation-defined attention networks, can modulate attentional processing and affect behavioral performance on sustained attention tasks. Of note, the finding that cerebellar connections were found to be highly predictive of performance fits with recent work<sup>103–105</sup> that has shown that cerebellar regions are both functionally connected to and can alter connectivity across large-scale cortical networks, such as the dorsal attention and default networks.

As research has shown that disparate regions across the brain are involved in sustained attention, we note that other avenues of research are seeking to understand how communication occurs across regions that fall within and across neural networks. What gives rise to functional networks that are not directly connected through white matter tracts, and how is structural connectivity related to functional connectivity more broadly? Do neural oscillations/synchrony drive the observed fMRI connectivity? While a full assessment of this topic is beyond the scope of the present review, the interested reader is referred to a recent review by Clay-

ton *et al.*<sup>106</sup> on the role of oscillatory signals in coordinating activity within and across neural networks. In particular, research in this area suggests an important role for low-frequency fluctuations and phase synchronization in coordinating processing within and across networks. Similarly, recent work has shown that frontal theta power may be a marker of trial-to-trial attentional fluctuations.<sup>62</sup>

### *Life span changes in sustained attention ability*

Just as research has highlighted the fact that sustained attention is not a static state, so too does sustained attention vary within the normal population and across an individual's life span. Behaviorally, there have been a few recent studies that have sought to characterize life span trends in sustained attention ability.<sup>54,107</sup> One large web-based study<sup>54</sup> of over 10,000 participants who completed the gradCPT task highlighted that sustained attention abilities develop over the course of childhood and young adulthood and do not begin to show age-related declines until one's mid-40s (Fig. 7). This is notable, as most cognitive abilities, such as fluid intelligence and processing speed, peak before one's 30s.<sup>108</sup> Consistent with this, a review<sup>109</sup> showed a general shift across adulthood ( $\geq 40$ s) in the activation of multiple networks (i.e., attention,<sup>110,111</sup> response inhibition,<sup>112</sup> performance monitoring,<sup>113</sup> and cognitive control<sup>110</sup>) moving from bottom-up stimulus processing involving more posterior and sensory areas toward greater top-down processing in frontal cortical and frontal subcortical networks, consistent with later maturation of frontal cortical regions.<sup>114</sup> Additionally, developmental changes in the default network have been observed showing increased long-range connections during development and greater deactivations throughout adulthood.<sup>109,111</sup> Given that the relative balance of task-positive and task-negative regions is directly related to task performance,<sup>52,57,92</sup> it is not surprising that sustained attention abilities evolve over time in line with the development of both frontal cortices and the default network. Comparing behavioral and neural data across the life span can also provide additional information for prediction analyses, as seen in a study that predicted sustained attention deficits on the basis of maturation curves of intrinsic functional connectivity.<sup>115</sup> While these late-maturing neural circuits may be directly related



**Figure 7.** Life span trends in sustained attention performance. Sustained attention performance of 10,430 participants who completed a web-based version of the gradCPT task grouped into age bins such that over 100 participants were represented in each age bin. Results are shown separately for reaction time variability, mean reaction time, discrimination ability ( $d'$ ), and criterion. Error bars show 95% confidence intervals. Solid lines show the best-fitting functions from a hierarchical regression analysis using segmented linear functions. Gray bars show the 95% confidence intervals for the estimated break points. Reaction time variability is defined as the coefficient of variation (CV; the standard deviation divided by the mean reaction time). Figure is adapted with permission from Ref. 54.

to late-peaking sustained attention ability, it will be interesting for future work to explore the role of motivation in age-related changes in attention and other aspects of cognition.<sup>116</sup>

### Deficits in sustained attention ability: clinical populations

Sustained attention difficulties have been associated with a diverse array of patient populations, including patients with developmental disor-

ders (ADHD,<sup>117–123</sup> autism<sup>124–128</sup>), acquired brain injury (hemispatial neglect,<sup>66,129–132</sup> traumatic brain injury<sup>19,133–136</sup>), neurodegenerative diseases (Parkinson's,<sup>137,138</sup> Alzheimer's,<sup>139,140</sup> multiple sclerosis,<sup>141–143</sup> age-related cognitive decline<sup>107,144,145</sup>), and psychiatric disorders (depression,<sup>146,147</sup> posttraumatic stress disorder,<sup>148,149</sup> bipolar disorder<sup>150–152</sup>). It is notable that recent functional neuroimaging work has shown that sustained attention deficits in



these clinical populations are associated with a range of changes in neural functioning, in many cases outside the traditional networks supporting attention. These sustained attention-related alterations in functioning have found specific changes in default,<sup>123,134,153</sup> limbic,<sup>102,147</sup> and cerebellar<sup>147</sup> regions, consistent with recent findings in healthy individuals<sup>57,92,102</sup> that sustained attention involves more than the salience and dorsal attention networks or the vigilance network,<sup>3</sup> as outlined above. This further highlights the variety of ways in which the distributed neural mechanisms supporting sustained attention can be disrupted. This also raises the important issue of assessing sustained attention reliably and accurately in the clinic, particularly because sustained attention deficits may be responsible for or exacerbate higher-level deficits in executive function, memory, or learning. While progress has been made in developing sustained attention assessments for particular populations,<sup>154</sup> there is currently not a single widely accepted clinical assessment that is sensitive to sustained attention deficits across the diverse array of patient populations. This is an important goal for future sustained attention research.

Researchers have long appreciated that sustained attention deficits are a core aspect of hemispatial neglect, a common disorder that typically occurs after right hemisphere damage. Though hemispatial neglect manifests as a disorder of spatial attention, nonspatial attention deficits<sup>19,131,132</sup> have been consistently shown to predict the chronicity and severity of spatial attention deficits.<sup>155</sup> Patients suffering from hemispatial neglect also show significantly steeper vigilance decrements compared with a matched stroke control group.<sup>156</sup> Recent work has highlighted that these sustained attention deficits may stem from some combination of reduced overall attention/working memory capacity and impaired motivation systems, all important components of the resource-depletion, resource-control, and opportunity-cost models. For example, patients' spatial attention deficits are exacerbated under a variety of dual-task conditions that tax attention and working memory.<sup>157</sup> Additionally, motivational deficits, which make neglect patients extremely difficult to rehabilitate, may also play key roles in patients' sustained attention deficits. Recent intervention work has highlighted how reward contingencies and playing rewarding

music can improve both spatial and nonspatial symptoms of neglect.<sup>158,159</sup> Current research is focused on elucidating the mechanisms of these sustained attention deficits and how they exacerbate spatial biases and impede recovery.

Though not as severe as in hemispatial neglect, age-related cognitive declines in sustained attention have also been consistently demonstrated.<sup>54,107</sup> Recent evidence and a new theoretical model suggest that the ability to successfully sustain attention throughout one's life could serve as a protective factor, possibly contributing to neural/cognitive reserve in the face of neurodegeneration and cognitive decline.<sup>160,161</sup> In particular, Wilson *et al.*<sup>162</sup> notably demonstrated that autopsy evidence linked neuronal density in the LC, the brain's main source of norepinephrine, which is involved in sustaining attention and arousal, to higher baseline functioning and slower cognitive decline before death.<sup>162</sup> This has inspired the hypothesis that the noradrenergic system, sustained attention, and perhaps the right hemisphere more generally are key components of cognitive/neural reserve.<sup>161</sup> Robertson<sup>161</sup> suggests that sustained attention may provide a gating mechanism wherein one is able to get more stimulation out of environments/situations/interactions and may help mitigate age-related cognitive decline. It also could be that being able to maintain a more optimal attentional state could allow one better access to learning and memory abilities. On the neural side, noradrenergic modulation has been linked with increased connectivity between right rather than left frontoparietal networks.<sup>163</sup> Furthermore, structural<sup>164</sup> and functional imaging<sup>165</sup> studies have particularly implicated loss of structural integrity and/or reduced engagement of right hemisphere regions as being related to cognitive decline with age. The associations between sustained attention, the noradrenergic system/right frontoparietal regions, and cognitive/neural reserve and the potential sources of these links are an exciting avenue of future aging research.

The myriad ways in which sustained attention can be disrupted and the extensive interplay of neural networks that are involved in successfully sustaining attention raises the question of whether there is a single optimal cognitive/neural state, with many ways to deviate from this state, or whether there are multiple neurocognitive approaches to successfully sustain attention. Increasing our understanding of

how disruptions to sustained attention networks affect sustained attention ability will provide crucial information, both theoretically, in terms of what successful sustained attention means, and clinically, in terms of developing novel ways to treat sustained attention deficits that may accompany various clinical disorders.

### Modulating sustained attention ability

Momentary lapses during sustained attention are extremely common and typically benign, but in certain circumstances they can have life-threatening consequences. For example, lapses have been associated with motor vehicle and operator-related train accidents.<sup>166–168</sup> Additionally, persistent deficits in sustained attention can have far-reaching negative impacts on quality of life. Recently, several novel lines of research have suggested that it is possible to enhance sustained attention, which has important implications for reducing lapses and improving clinical outcomes. Broadly, research on improving sustained attention ability falls within three categories: (1) cognitive/behavioral training, (2) psychopharmacological, and (3) biofeedback/brain stimulation.

In terms of cognitive training, several different approaches have been devised to enhance sustained attention. One of the benefits of targeting sustained attention is that it underlies or provides a gating mechanism to other cognitive abilities, such as executive functions and learning. Thus, enhancing sustained attention could generalize to improvements in several other aspects of cognition, a phenomenon that is a rarity among cognitive training programs.<sup>169,170</sup> Meditation training is the oldest and most widely used method to improve sustained attention. Though evidence for some forms of meditation improving sustained attention have been mixed (e.g., mindfulness-based stress reduction<sup>171</sup>), focused-attention meditation training has consistently been shown to improve sustained attention in a variety of populations.<sup>172</sup> Providing strong evidence for generalization, meditation training has also been associated with a variety of improvements beyond sustained attention, including executive control,<sup>173</sup> self-regulation,<sup>174,175</sup> and mood<sup>176</sup> and may affect the structural integrity of brain regions critical for sustained attention.<sup>177</sup> Computer-based cognitive training programs that target cognitive control<sup>178</sup> or directly target sustained attention

(e.g., tonic and phasic alertness/attention training (TAPAT)<sup>179</sup>) have also been shown to enhance sustained attention and generally improve cognition. For example, TAPAT has shown to improve sustained attention in hemispatial neglect,<sup>129,179</sup> Parkinson's disease,<sup>138</sup> and healthy aging<sup>180</sup> while also improving spatial attention and executive functions in these populations. Together, this suggests that one's ability to sustain attention is highly trainable and that improvements in cognitive training can result in more general cognitive improvements. Additional studies characterizing the mechanisms of this generalization (e.g., promoting a better attentional state versus increasing attentional resources versus increasing motivation) would be useful in further developing these interventions.

There already exists an extensive literature on psychopharmaceuticals in the treatment of attention deficits, and a full review is beyond the scope of this article. Pharmaceuticals that primarily target the noradrenergic system (e.g., guanfacine) or catecholamine system in general (e.g., methylphenidate, amphetamine, modafinil) have consistently been shown to improve wakefulness and sustained attention in a variety of populations, including children and adults with ADHD,<sup>181</sup> patients suffering from hemispatial neglect,<sup>182</sup> and healthy adults.<sup>183</sup> Research suggest that the effects of therapeutic doses of these pharmaceuticals are relatively specific to the prefrontal cortex, strengthening its functioning and interactions with other brain regions.<sup>184</sup> In addition to catecholamines, we also note recent interest in the role of the cholinergic systems in top-down attentional control processes.<sup>185,186</sup>

While pharmaceutical interventions can globally affect neural processing, an alternative physiological approach is localized brain stimulation of cortical regions associated with attention. Work into the effectiveness of brain stimulation to increase a variety of cognitive domains is currently underway.<sup>187,188</sup> These approaches combine new knowledge regarding the neural networks that support cognition and test whether stimulation of network nodes in conjunction with cognitive training protocols can improve performance in both clinical<sup>189</sup> and nonclinical<sup>187,190</sup> populations. For example, a recent study<sup>190</sup> showed that transcranial direct current stimulation over the right dorsolateral prefrontal cortex reduces the vigilance decrement in healthy participants. Transcranial magnetic

### Box 1: Outstanding questions and future directions for research on sustained attention

1. How do brain regions outside of the classic vigilance networks (e.g., cerebellum) contribute to sustaining attention?
2. Is there one optimal attentional state or are there many approaches to successfully sustain attention? Additionally, is there an optimal brain state?
3. What is the role of the default mode network in sustained attention? Can we reconcile the seemingly conflicting roles of the default mode network in mind wandering and behavioral stability?
4. Do the underlying cognitive mechanisms that explain attention failures (mind wandering, motivation, resources) differ across individuals and/or clinical populations, and, if so, can this lead to more individualized cognitive interventions?
5. Similarly, do the underlying neural mechanisms that explain attention failures differ across individuals/clinical populations, and can this discovery lead to individualized neurostimulation-based interventions?

stimulation targeting network-specific cerebellar regions has been shown to change functional connectivity in dorsal attention and default networks, indicating an exciting potential method for enhancing attention.<sup>103</sup> Finally, other studies are developing algorithms to provide real-time feedback on neural activity,<sup>191–193</sup> with initial results suggesting that these approaches may help individuals to monitor and adjust their attentional focus. For example, real-time fMRI, where BOLD response is analyzed to provide near-simultaneous feedback regarding attentional state (attention focused or distracted), has been used to train attention in healthy subjects and could potentially help remediate attentional biases in affective disorders.<sup>194</sup>

### Summary

Sustained attention research has been active for over 60 years, and the last 5 years have been no exception. Conceptually, questions remain regarding how to define sustained attention and why sustaining focused attention is challenging to individuals (Box 1). Recent cognitive models, including the resource-control<sup>27</sup> theory, incorporate behavioral findings that task engagement, motivation, and reward can modulate overall performance as well as performance decrements over time by suggesting that attentional resources do not decline *per se*, but rather there exists a subjective cost to devoting cognitive resources to one task, which tends to increase over time. This cognitive model, however, conceptualizes control failures as arising from executive control functions, which are distinct

from attentional resources. An open question that remains, however, is whether these conceptually distinct systems have differential neural bases. Toward answering these questions, an emerging body of literature<sup>52–54,57</sup> has begun to characterize the fluctuations in sustained attention over finer timescales with concurrent neuroimaging. Along with many of the task-positive regions identified in a recent meta-analysis of sustained attention,<sup>3</sup> these studies have highlighted extensive interactions across multiple networks and the important role that default network regions may play in supporting sustained attention generally,<sup>52,57,64,92,102</sup> predicting overall sustained attention ability<sup>102</sup> and trial-by-trial lapses.<sup>57,92</sup> These studies highlight an important change in our conceptualization of the neural bases of cognition. Just as focusing and sustaining attention does not occur in an isolated state, but rather operates within and is influenced by the sensory stimuli from the external environment and the emotional and cognitive states of an individual, so too must the neural mechanisms that engage and maintain sustained attention operate in conjunction with and be influenced by all of the other sensory and cognitive processes that occur over time.

In addition to basic research on sustained attention, studies of clinical populations show that sustained attention deficits are common across a wide range of neurological<sup>19,56,189,195</sup> and psychiatric disorders.<sup>196</sup> Emerging evidence suggests that sustained attention deficits are accompanied by changes in neural functioning across a wide range of areas, leading to the suggestion that, while there

may be one optimal way to be on task, there are many ways in which sustained attention can be disrupted or suboptimal. Future work in this area will continue to provide new information about potential biomarkers to help identify individuals with sustained attention deficits and to tailor treatments to their specific marker of dysfunction. Whether with the aim of developing novel treatments or helping healthy individuals maximize their own potential, gaining a better understanding of the complex network interactions that support the ability to sustain attention remains an important and active research area in cognitive neuroscience.

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## Competing interests

The authors declare no competing interests.

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