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The Prosthetics of Vigilant Attention: Random Cuing Cuts Processing Demands

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Objective: Engagement in tasks requiring vigilant attention is susceptible to modulation by exogenous stimulation, reflected in changes in performance accuracy and speed. The shift from endogenous to exogenous control may be observed not only when the external cue is meaningful to the task, but also when it holds no information about the task or performance. The purpose of this study was to examine how the shift to exogenous engagement is reflected in changes to the well-documented, right-lateralized, frontal-parietal-thalamic vigilant attention network. ***Method:*** Using functional magnetic resonance imaging , healthy participants were scanned as they performed the Sustained Attention to Response Task (SART) in 60-s blocks, some of which were presented with brief, random, auditory tones. The SART requires participants to overcome the tendency to respond in an automatic, task-driven manner in response to infrequent no-go stimuli. ***Results:*** Despite no overall effect on performance, and only a transient increase in response times immediately following the tones, the SART with alerting tones was associated with a diminished pattern of activation in key nodes of the network. The pattern of right-lateralized activity observed with the SART was attenuated with the tones, and activity in the right middle frontal gyrus was significantly diminished, as revealed by region-of-interest analyses. ***Conclusions:*** Alerting tones provided the stimulation to cue the maintenance of the goal-state, reducing reliance on prefrontal control mechanisms and demonstrating the shift from endogenous top-down control to exogenous control. These findings suggest a neural mechanism for the facilitatory effects of exogenous engagement for patients with damaged top-down attentional brain systems.

Keywords: fMRI, alerting tones, SART, DLPFC, sustained attention, arousal

Sustained attention, also known as alertness or vigilance and more recently as vigilant attention (Robertson & Garavan, 2004), functions to maintain goal-directed behavior by developing and maintaining a state of response readiness over time (Manly & Robertson, 1997). Contemporary models of attention have included sustained attention as a major component process. The alerting circuit, described in Posner and Petersen's (1990) influential model of attentional control systems, is implicated in sustaining attention in order to process high priority signals. This system is thought to be distinct from, but highly interdependent with, the orienting and anterior circuits, responsible for selective and executive aspects of attentional control. The alerting and orienting circuits of the Posner and Petersen model, both subserved in part by the parietal cortex, have been shown to have independent influences on reaction times in experiments involving both alerting and orienting stimuli (Fan, McCandliss, Sommer, Raz, & Posner, 2002; Fernandez-Duque & Posner, 2001). Like orienting, sustained attention is subject to the influences of both exogenous and endogenous control mechanisms. When external stimulation is introduced, a shift in arousal is induced that contributes to sustained attention processing and is reflected in performance. Paus and colleagues (1997) demonstrated the interactive nature of arousal and attention in their electroencephalography/positron emission tomography (EEG/PET) study of changes in brain activation over time. With time on task, activation in key right-lateralized cortical areas, anterior cingulate, thalamus, and midbrain reticular formation decreased, suggesting a network that mediates a decline in sustained attention over time. Furthermore, activity in the right cortical and the anterior cingulate/thalamic/midbrain networks covaried independently from one another, suggesting distinct networks for attentional control and arousal, respectively. Robertson and Garavan (2004) argue that the ascending network of arousal and top-down network of effortful maintenance of goal representations may form two separate but interactive components of the vigilant attention system, with changes in performance reflecting a shift from endogenously mediated control to increased reliance on exogenous support and vice versa. Mottaghy et al. (2006) delineated an ascending alerting network (brainstem and thalamus) and a right frontal-parietal network of intrinsic

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alertness that converge on and are coordinated by activity of the anterior cingulate cortex. Whether bottom-up arousal and top-down alertness networks are truly independent (but highly interactive), or part of a unified alerting and sustained attention system (Sturm & Willmes, 2001), the foregoing suggests that these elements of sustained attention can be modulated by different task demands.

The neural basis of endogenous control of sustained attention has been well researched, with human neuropsychological and neuroimaging studies revealing a right-lateralized network of brain regions (Cohen et al., 1988; Coull, Frith, Frackowiak, & Grasby, 1996; Manly et al., 2003; Pardo, Fox, & Raichle, 1991; Paus et al., 1997; Rueckert & Grafman, 1996, 1998; Sturm et al., 1999; Whitehead, 1991). The right dorsolateral prefrontal cortex (DLPFC) is consistently implicated as a key functional region, likely the site of top-down control. Results often point to a role for the parietal cortex, both superior and inferior, the anterior cingulate cortex, and it is likely that subcortical structures play a role in the induction of arousal that is necessary for efficient sustained attention performance, most notably the thalamus. Less is known about the impact that external stimulation has on sustained attention processing and its underlying neural activity. In one influential model, a ventral frontal-parietal network mediates orienting of attention to unexpected stimuli, acting as a "circuit-breaker," interrupting top-down processes mediated by the dorsal system in response to task-important stimuli (Corbetta, Patel, & Shulman, 2008; Corbetta & Shulman, 2002). A network of thalamic-mesencephalic regions may be also be engaged in phasic or exogenous alerting that occurs when sustained attention is externally enhanced via a warning signal (Fernandez-Duque & Posner, 2001). The interaction of endogenous and exogenously controlled attention is demonstrated by studies involving the presentation of periodic alerting tones. For example, alerting tones eliminate the right hemisphere advantage seen when targets were presented in the left visual field (Whitehead, 1991) and they help patients with neglect due to right-lateralized damage overcome unawareness of visual events presented to the left visual field, presumably through the recruitment of the preserved thalamic-mesencephalic phasic alerting circuit (Robertson, Mattingley, Rorden, & Driver, 1998). The resumption of tonic alertness following phasic orienting is likely mediated by prefrontal cortex (Fassbender et al., 2006; Kubler, Dixon, & Garavan, 2006).

In order to investigate the impact of exogenous stimulation on sustained attention and its associated neural network, we utilized the Sustained Attention to Response Task (SART) and functional magnetic resonance imaging (fMRI). Most traditional vigilance tasks require monitoring for targets during long, inactive intervals; the infrequent target situated within target-free intervals itself may serve as an exogenous trigger (Robertson, Manly, Andrade, Baddeley, & Yiend, 1997). The SART, on the other hand, requires sustained, rapid responding over a series of targets such that upon the detection of a nontarget, the more automatic, task-driven response must be inhibited. Specifically, participants are presented with sequences of repetitive visual stimuli at an invariant rate and are required to respond to each trial with a key press. Nontargets are presented randomly among the targets and participants are instructed to inhibit responding upon detection. The SART is designed explicitly to place high demand on the sustained attention subsystem and to induce action slips or absentmindedness. The operations involved in the SART may be more suitably described as maintaining goal-directed behavior over time with simultaneous continuous inhibition of task irrelevancies. Robertson and Garavan (2004) term this conceptualization of SART processes as vigilant attention, reflecting the overlapping executive processes involved.

Accordingly, SART performance is predictive of everyday attentional failures in healthy participants (Robertson, Manly et al., 1997) and can discriminate between groups of normal and traumatically brain injured adults (Dockree et al., 2004; Manly et al., 2004; O'Keeffe, Dockree, & Robertson, 2004; Robertson, Manly et al., 1997). The tonic sustained attention elements of the SART are associated with activation of right frontal-parietal regions (Fassbender et al., 2004; Manly et al., 2003). These findings have been elaborated in EEG studies indicating alpha wave desynchronization (suggestive of increased attentive processing) immediately preceding a SART no-go trial (Dockree et al., 2004), reduced amplitude P300 during periods of mind wandering (Smallwood, Beach, Schooler, & Handy, 2008), and distinct ERP components over occipital, parietal, and frontal regions associated with various SART elements, including error evaluation and goal recollection (Dockree, Kelly, Robertson, Reilly, & Foxe, 2005; Zordan, Sarlo, & Stablum, 2008).

Of particular relevance to the current study is a series of SART experiments conducted by Manly and colleagues (2004) that examined the behavioral effect of exogenous alerting on SART performance. Random tones, holding no predictive information about the upcoming trials, were found to reduce errors and transiently increase response times, but have no overall effect on speed of responding. This pattern of results suggests that the tones serve an interrupting function that accommodates successful performance, possibly indicating reengagement of supervisory control. However, these effects can be accounted for by an increase in phasic alertness as well. Recent work has shown that declining alertness results in a rightward attentional bias with the flagging of the right-hemisphere vigilant attention system (Dodds et al., 2008; Manly, Dobler, Dodds, & George, 2005).

We examined the influence of random alerting tones on the functional neuroanatomy of SART performance in order to explore the neural impact of exogenous engagement on vigilant attention. The design facilitated a comparison of the impact of random alerting tones at the task level, eliciting vigilant attention processing presumably maintained over the course of 60-s blocks. We hypothesized that alerting tones would reduce the need for endogenous engagement of the right frontal-parietal vigilant attention system, revealing a pattern of reduced activation of this network with concomitant increases in subcortical structures, including thalamus, reflecting increases in arousal.

Methods

Participants

The sample comprised 10 healthy, English-speaking adult volunteers (six male; mean age = 28.4 years). Volunteers were excluded from participation if they had a history of neurological injury or disease, alcohol or drug abuse, psychiatric illness, or current use of prescription medications with side effects known to alter arousal, memory, or ability to follow instructions. Those unable to undergo MRI scanning due to pregnancy, report of claustrophobia-like symptoms, body size, or presence of ferrous material on or in the body unfixed to bone were also excluded.

Informed written consent was obtained upon first face-to-face contact with the participants. Participants were paid $50 following the fMRI scan. All procedures received prior approval of the Sunnybrook Health Sciences Centre Research Ethics Review Board and the Joint Baycrest /University of Toronto Research Ethics Review Board, in compliance with the ethical standards of the 1964 Declaration of Helsinki. Informed written consent was obtained from each participant prior to their inclusion in the study.

Procedures

Testing. The scanning task involved SART and control blocks. The original SART requires participants to respond with a key press to digits from 1 to 9 appearing on a computer screen for 250 ms followed by a 900-ms mask. Participants are instructed to withhold their response to a specified "no-go" target, the digit "3." The importance of both speed and accuracy are emphasized to the participant. Digits are presented at random, 25 times each. Therefore, the total duration of the task is 4.3 min. For imaging, presentation of the standard SART was adjusted to fit the constraints imposed by the nature of the brain's hemodynamic response as measured by fMRI. Three blocked series were scanned. Series comprised a total of nine 60-s blocks, randomly presented and separated by a 15-s interval. Each of the series contained two SART blocks, two control blocks, two SART blocks with tones, two control blocks with tones, and one fixation block. Stimuli were presented using E-Prime 1.0 stimulus presentation software (Schneider, Eschman, & Zuccolotto, 2001).

SART block. Limited to 60 s in length, the SART block comprised 52 trials presented at a rate of 1 every 1150 ms. Therefore, "no-go" or inhibition trials (the digit "3") were presented 5.7 times on average per SART block. Although the 60-s block length is shorter than that of the standard SART, a previous PET study has shown that a reliable signal can be obtained from a SART block of 103.5 s in length (Manly et al., 2003).

Control block. The control block was designed to reduce the sustained attentional demands of the task while continuing to evoke the visual and motor processes of the SART block. Therefore, the control blocks comprised 52 trials presented at a rate of 1 every 1150 ms, but the participants were instructed to respond to every digit, including the previously specified "no-go" target.

SART & control blocks with alerting tones (SART + tone, Control + tone). In these blocks, 30 ms alerting tones of 1975Hz were randomly presented every 8 to 12 s (an average of 10 s between each tone). Participants were exposed to the tone condition during the practice session and they were informed that the purpose of the tone was to remind them to focus on what they are doing.

Throughout each of the blocks, a cue remained on the screen (centered above the digits) to remind the participants of the condition. In the SART conditions, the cue read "withhold 3." In the Control conditions, the cue read "press all." Overall, as each blocked series was 11 min and 20 s in length, the total imaging time for each participant was approximately 34 min.

Prior to the scanning session, participants were introduced to the SART and control conditions during a brief practice session presented on a laptop computer. Participants were instructed to respond as quickly and accurately as possible and were given the opportunity to practice 60 s of each of the SART, Control, and SART with alerting tones conditions.

Data collection. Imaging was performed with a 1.5 T scanner using a standard head coil (CV/I hardware, LX8.3 software; General Electric Medical Systems, Waukesha, WI). A three dimensional fast spoiled gradient echo pulse sequence (TR = 12.4 ms, TE = 5.4 ms, flip angle 35 deg, 22 × 16.5 cm FOV, 256 × 192 acquisition matrix, 124 axial slices, 1.4 mm thick) was used to acquire a T1-weighted volumetric anatomical MRI for each participant. Functional scans were obtained using a single shot T2*-weighted pulse sequence with spiral readout, achieving 24 slices, 5 mm thick (TR = 2000 ms, TE = 40 ms, flip angle 80 deg, 90 × 90 effective acquisition matrix, 20 cm FOV).

Stimuli were presented on a back-projection screen using an LCD projector (Model 6000, Boxlight Corp., Poulsbo, WA.). Participants viewed the stimuli using angled mirrors mounted on the head coil. Auditory stimuli were delivered through circumaural headphones. Participants responded using a response pad connected to a computer located outside the magnet room. Reaction times and accuracy of responses were recorded.

Analysis

Functional neuroimaging data preprocessing and analysis were performed using the Analysis of Functional Neuroimages software package (AFNI version 2005 12 30 0934; (Cox & Hyde, 1997). Following motion and slice-timing correction and coregistration to the anatomical scan, time-series data were submitted to a deconvolution analysis using the AFNI plug-in 3dDeconvolve. A general linear model was applied to the functional data to derive parameter estimates and corresponding t-statistics for the impulse response functions corresponding to the four experimental conditions. The resulting whole brain, voxel-based, activation maps were transformed into standard space (Talairach & Tournoux, 1988) and smoothed (6 mm filter, fwhm) prior to group analysis, in which mean changes in signal intensity associated with the task conditions were analyzed using mixed effects (conditions fixed, subjects random) two-factor analysis of variance (ANOVA). Comparisons included SART versus Control, SART versus SART + tone, SART + tone versus Control + tone, and Control + tone versus Control. For task comparisons, a combined threshold for individual voxel probability was set of $p < .001$ and a minimum cluster size of 150 μl (three contiguous voxels).

A hypothesis-driven region-of-interest (ROI) analysis was conducted to examine the effect of the tone on the right DLPFC activation elicited by the SART. Beta values for the peak right DLPFC voxel identified in the SART versus Control condition were extracted for the four conditions (SART, SART + tone, Control, Control + tone). Differences in right DLPFC activation across these conditions were assessed with repeated measures ANOVA.

Results

Behavioral

Errors of commission. SART responses were considered errors of commission if the participant failed to withhold responding during the presentation of the nontarget (the digit "3"). The addition of the alerting tone did not significantly affect the mean number of errors of commission made, $F_{(1,9)} = .08$, $p = .78$; effect size: partial $\cdot\eta^2 = .009$, (see Table 1).

Table 1
Response Times and Errors by Condition

Condition	N	Response times Mean (ms)	Response times SD	Errors Mean	Errors SD
SART	10	346.98	65.76	2.24	1.17
Control	10	220.08	95.87	N/A	N/A
SART + tones	10	352.87	72.01	2.19	1.30
Control + tones	10	249.36	73.54	N/A	N/A

Response times. Mean response times for the SART were calculated for those trials in which participants responded accurately to the presentation of a target (all digits except "3"). Response times to nontargets were not included in this analysis. Significant main effects of condition, $F_{(1,9)} = 79.45$, $p < .0001$; effect size: partial $\cdot\eta^2 = .898$, and tone, $F_{(1,9)} = 5.28$, $p = .0471$; effect size: partial $\cdot\eta^2 = .370$, on response times were found. Post hoc analysis (Tukey's HSD) revealed that participants responded more slowly during the SART conditions than the Control conditions. Likely due to a lack of power, the main effect of tone was not clarified by a significant interaction between condition and tone, $F_{(1,9)} = 2.27$ $p = .1658$; effect size: partial $\cdot\eta^2 = .202$, but the effects of the tone on the SART and Control conditions were not parallel. The tone had a greater effect on the Control condition than the SART; participants responded slower when tones were presented during the Control condition (see Table 1).

We suspected the tone may have had a transient effect on response times that was not apparent when mean response times across entire blocks were compared. Indeed, repeated measures ANOVA revealed that within blocks of SART or Control with random tones, response times were significantly slower immediately following a tone compared to those of trials immediately preceding a tone. Mean pretone response times for SART and Control, 345 and 253 ms, respectively, were significantly slowed to 367 and 270 ms, respectively, $F_{(1,9)} = 7.16$, $p = .025$; effect size: partial $\cdot\eta^2 = .443$.

Imaging Findings

SART > Control. The SART condition, relative to the Control, was associated with robust patterns of activation in hypothesized areas (see Table 2 and Figure 1). As predicted, the SART, relative to the Control, elicited areas of peak activation in the right middle frontal gyrus (BA 9) and right thalamus (medial dorsal nucleus and pulvinar). SART activity in the expected right parietal lobule (BA 40) was detected, however the cluster size was subthreshold (41 μl).

SART + tone > Control + tone. To examine the impact of the tone on the SART-related activity described above, controlling for the motor and visual processes, we contrasted the activity elicited by the SART + tones to that of the Control + tones. This comparison resulted in only one small area of activation in left middle frontal gyrus (see Table 2) and no significant activity in the hypothesized right frontal, parietal, and thalamic regions, suggesting that alerting tones diminish the robust activations associated with the SART relative to the Control.

SART > SART + tone. Given the effects described above, we sought to clarify the effect of tone presentation on brain activity associated with the SART, specifically that the right-lateralized frontal-parietal-thalamic network is activated with the SART and diminished with the tones. In order to confirm these patterns of activation, we contrasted the two SART conditions directly, expecting to observe activity in key right frontal, parietal, and thalamic regions with the SART over that of the SART + tones. In fact, small areas of activation were observed with peaks in the critical right frontal, parietal, and thalamic regions, but these were well below cluster size threshold. Only two significant clusters that met cluster threshold were active with the SART relative to the SART + tone in the left caudate and left medial frontal gyrus (see Table 2).

Control > Control + tone. When the two Control conditions were compared to determine the effects of the tone on brain activation that are independent of the intense sustained attention demands of the SART, brain regions activated with Control + tone relative to the Control included the left middle frontal gyrus (BA 6), the right cerebellum, and the right postcentral gyrus (BA 2). A small area of right inferior parietal lobule (BA 40) was also activated in association with the Control + tone condition. This finding suggests that a component of the vigilant attention network, the right inferior parietal lobe, becomes active during the low-demand Control task when tones are presented.

ROI analysis. The whole-brain analysis detailed above showed robust activity in the right middle frontal region in association with the SART but no significant activity in this region associated with the SART + tones. To further explore the apparent attenuation effect of the tone, we selected the voxel of peak activation in this region (x, y, z = 36, 27, 36) for ROI analysis. We found no main effect of condition or tone but a significant condition x tone interaction, $F_{(1,9)} = 6.17$, $p = .035$, (see Figure 1). Post hoc analysis (Tukey's HSD) revealed that activation in this region is significantly diminished by the tone during SART performance ($t = 2.3$, $p = .004$). Mean intensity in this region was lowest during the Control condition. When the Control condition was performed with tones, right middle frontal activation increased but this difference did not reach significance ($t = -1.4$, $p = .19$). Similar significant interactions were not found when ROIs of key thalamic and parietal regions were selected and subjected to the same analyses.

Discussion

The capacity to maintain a sustained or vigilant attentive state is modulated by endogenous and exogenous factors, yet the influence of these factors on task-related brain activity has received little attention. In this study, random alerting tones, designed to provide no feedback or information about upcoming events, were

Table 2
Summary of Brain Regions in Which Task-Related Comparisons Revealed Significant Activations

			SART > Control				SART + tones > Control + tones				SART > SART + tones				Control + tones > Control			
Region	R/L	BA	Max	X	Y	Z	Max	X	Y	Z	Max	X	Y	Z	Max	X	Y	Z
Frontal																		
Middle frontal	L	6	6.7	−14	−8	59	7.4	−25	−12	45					17.3	−43	−1	50
	R	9	7.9	36	27	36												
Inferior frontal	R	13/47	6.7	45	26	4												
Medial frontal	L	10									6.4	0	63	13				
Parietal																		
Postcentral gyrus	R	2													6.8	46	−26	40
Paracentral lobule	R	5	6.0	5	−41	49												
Posterior cingulate	L	30	6.2	−20	−64	9												
	R	29	7.6	12	−39	16												
Precuneus	L		8.3	−24	−42	39												
Inferior parietal lobe	R	40	*5.9**	*54*	*−36*	*30*									7.2	38	−49	51
Temporal																		
Parahippocampal gyrus	R	36	7.7	26	−33	−13												
Occipital																		
Middle occipital	L	31	8.0	−26	−76	16												
	R		7.0	30	−63	6												
Inferior occipital	R	19	6.4	31	−83	−5												
Subcortical																		
Thalamus (MD & pulvinar)	R		11.9	10	−23	9												
Caudate	L		6.1	−20	−4	23					8.6	−14	11	12	9.4	−35	−23	−2
Putamen	R		5.8	23	11	10												
Cerebellum																		
	R		8.8	10	−61	−20									8.9	12	−32	−33
			5.8	17	−47	−16												
			7.5	−9	−51	−35												

Note. Max = Maximum t-statistic at peak coordinate; X Y Z = Coordinates in standard space; BA = Brodmann Area; MD = medial dorsal nucleus.
* Indicates sub-threshold cluster.

the source of exogenous modulation during a task requiring a high-level of endogenous control, the SART. The neural network elicited by the SART was attenuated in the presence of tones. Activity in a key node of this network, the right DLPFC, was diminished significantly with tone presentation, reflecting the important role of this region as vigilant attention is modulated via both endogenous and exogenous means.

Endogenous Engagement During SART Performance

The SART is a task of high demand, with repeated rapid stimulus presentation requiring responses under time pressure (Manly & Robertson, 1997). No time-on-task decrements are assumed because the vigilant attention operation is viewed as a system that endogenously refreshes itself on a short cycle (Robertson, Ridgeway, Greenfield, & Parr, 1997). The response time data are consistent with this theory. In the SART condition, response times were significantly slower than those of the Control, which was designed to elicit the high-speed motor and perceptual responses of the SART without the vigilant attention demands. This effect reflects the effortful, endogenous maintenance of the goal-state required during SART performance to overcome the tendency toward automatic responding (Robertson, Manly et al., 1997). In the Control condition, the faster response times reflect the induction of automatic, task-driven responses in the absence of a goal-state requiring a readiness to differentially respond. Therefore, the SART elicits vigilant attention processing that is not driven by exogenous task-related or environmental triggers.

A distinct, asymmetric neuroanatomical network was activated in the SART condition when compared to the Control condition. The overall pattern of activation revealed by the SART is generally consistent with previous neuroimaging investigations of sustained attention (Cohen et al., 1988; Coull et al., 1996; Hager et al., 1998; Manly et al., 2003; Pardo et al., 1991; Paus et al., 1997; Sturm et al., 1999). The activation of DLPFC, namely middle frontal gyrus (BA 9), corresponding to top-down control processes, is most consistent with other neuroimaging results (Cohen et al., 1988; Hager et al., 1998; Manly et al., 2003; Paus et al., 1997; Sturm et al., 1999). The thalamic activations were localized to peaks in mediodorsal nucleus and pulvinar. The thalamus is a critical subcortical structure involved in attention, in particular sustained attention and orienting. Kinomura, Larsson, Gulyas, and Roland (1996) demonstrated that thalamic and midbrain tegmental rCBF is higher during vigilance-CPT tasks than resting or self-paced motor response conditions. The pulvinar activation is consistent with other studies involving tasks of sustained responding with limited selection demands. Sturm et al. (1999) also found thalamic activation localized to the pulvinar associated with intrinsic alertness.

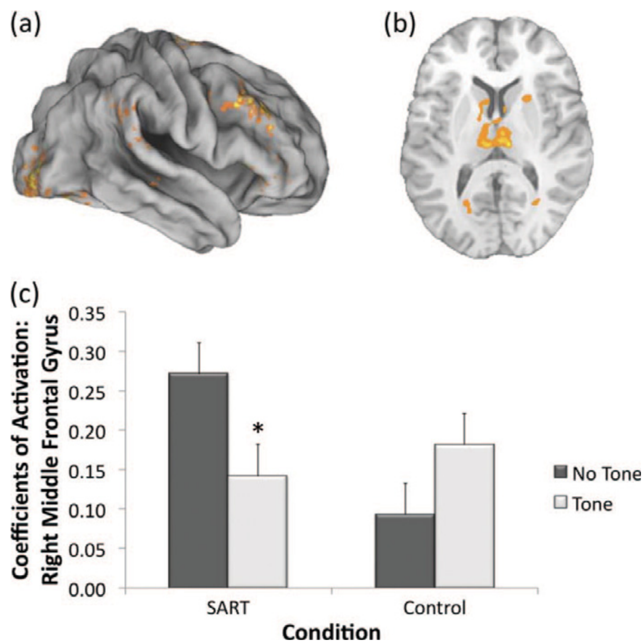

Figure 1. Brain images depicting significant activations associated with SART condition when compared to Control condition, including (a) right middle frontal gyrus (BA 9) and (b) bilateral thalamus. Co-ordinates and t-values are listed in Table 2. Images were thresholded at $p < .001$. (c) Region of interest analysis involving comparison of β-coefficients in the selected peak voxel of right middle frontal gyrus (x, y, z coordinates 36, 27, 36) by condition. Error bar values were calculated based on the pooled standard error of the tone and interaction terms in order to demonstrate simple effects comparisons, revealing a significant difference between the SART conditions with and without tones ($t = 2.3$, $p = .004$).

Recent studies have explored the overlapping and interacting nature of executive control mechanisms of the frontal lobes (De Pisapia & Braver, 2006; Fassbender et al., 2006; Marklund et al., 2007; Stuss et al., 2005). The right inferior frontal and bilateral middle frontal activations observed in this study in association with SART performance could reflect engagement of a common attentional network with sustained elements (Marklund et al., 2007) or the selection and response inhibition elements of the SART. In fact, vigilant attention has been considered as a process that requires continuous inhibition of task irrelevances, thus strongly overlapping functionally with response inhibition (Robertson & Garavan, 2004). Many studies of response inhibition have reported activity in frontal areas similar to those seen here (Garavan, Ross, Murphy, Roche, & Stein, 2002; Garavan, Ross, & Stein, 1999; Liddle, Kiehl, & Smith, 2001; Menon, Adleman, White, Glover, & Reiss, 2001), often attributed to inhibitory control of affective behavior (Roberts & Wallis, 2000). Selection undoubtedly plays a role in SART performance as correct inhibitions require the filtering out of irrelevant information, thus explaining the prominent activity of the pulvinar (LaBerge, 1990; Shipp, 2004), with the selection/working memory aspects of the SART and thus explaining the activity in bilateral DLPFC regions (Kastner & Ungerleider, 2000). Finally, the lack of significant parietal activation in the SART condition compared to the low-level Control condition could indicate that the parietal lobe is similarly active during both conditions, supported by the Control-Control-tone comparison, providing evidence that the parietal lobe is the site of interaction of the attentional subsystems and may mediate the expression of attention rather than control (Fernandez-Duque & Posner, 2001; LaBerge, 2005).

Exogenous Engagement During SART Performance

Randomly presented alerting tones were introduced during the SART to examine the effect of exogenous engagement on vigilant attention. The tone was hypothesized to affect performance by increasing arousal or through the interruption of automatic responding and facilitation of the resumption of supervisory attentional control (Norman & Shallice, 1986). In simple and choice reaction time tasks, a warning signal is thought to support phasic alertness, resulting in speeded response times (Parasuraman, Warm, & See, 1998). However, in the present study, the tones were designed to be noninformative or accessory cues as they did not provide any information about upcoming nontargets. The addition of alerting tones during SART performance did not result in a change in overall performance with respect to errors of commission or response times, possibly due to a combination of the high demands of the task and the brief duration of the stimulus block (60 s); performance benefits owing to the tone have been obtained with longer blocks (Manly et al., 2004). We did observe a transient slowing of response times on trials immediately following the tone, reflecting the interruption of automatic responding in favor of resumption of supervisory control (Manly et al., 2004).

The effect of alerting tones during the SART was also associated with a different pattern of neural activation, including attenuation of the right-lateralized vigilant attention network. Noticeably absent was activation in the right DLPFC. Further hypothesis-driven ROI analysis in this region confirmed that activity observed robustly with the SART was significantly reduced when the SART with tones was performed. The reduced activation suggests that the alerting tones provide stimulation to cue the maintenance of the goal-state exogenously, thus reducing the need for top-down attentional control mediated by the right DLPFC. A similar effect was seen in a study of a go/no-go task performed with random, noninformative visual cues in which the cues had no effect on performance but were associated with fewer right DLPFC and inferior parietal cortex activations than in the uncued condition (Fassbender et al., 2006).

A reduction in the need for top-down (right prefrontal) attentional control may explain why thalamic activation was reduced in association with the SART-tone task. The mediodorsal and pulvinar thalamic nuclei, with known afferent and efferent connections with prefrontal cortex (Goldman-Rakic & Porrino, 1985; Romanski, Giguere, Bates, & Goldman-Rakic, 1997), are believed to be part of the modulatory corticothalamic pathways that control the response modes of thalamocortical activity and mediate focused information processing (Sherman & Guillery, 1996), as suggested by the robust coactivation of the mediodorsal and pulvinar thalamic nuclei with right DLPFC during the SART blocks in this study. In the presence of alerting tones, however, requirements for endogenous attentional control are reduced. Thalamic activation also fell short of threshold in the SART-tone versus Control-tone and Control versus Control-tone comparisons.

SART performance was maintained when the tones were presented, despite the attenuation of the right prefrontally based sustained attention network. While the reduced reliance on this system can be attributed to the tones, there was no concomitant increase in other target areas that could support performance. Therefore, our data are inconsistent with the hypotheses that alerting tones activate the bottom-up thalamic-mesencephalic circuit or the top-down right prefrontal based system; both were attenuated in association with the SART-tone task. A different case can be made, however, for the Control task, where the alerting tones had a significant slowing effect on response times, both across blocks and transiently, and they were associated with increased activation in the left DFLPC, suggesting an orienting response to the tones, or an exogenous reorienting response via the ventral circuit described by Corbetta and Shulman (2002). The very low-demand Control task, designed to elicit sustained attention processing only minimally, was more vulnerable to the distraction of the irrelevant random tones and response times were less likely to recover fully following the distraction. In our ROI analysis, mean activity in the right DLPFC trended toward increased activity with Control-tone performance. Alternatively, the fact that the Control task is inherently more vulnerable to distraction places higher demand on inhibitory processing. The left DLPFC activity may be indicative of an inhibitory response to the random tones (Fassbender et al., 2004; Kelly et al., 2004; Menon, Adleman, White, Glover, & Reiss, 2001).

Considering the behavioral and neural effects of the tone on the SART and Control tasks, the nature of the tone effects appears to be dependent on the degree of endogenous engagement elicited by the task. When vigilant attention is high, as in the SART, the strong external stimulation lessens top-town control, attenuating the sustained attention network to the level of the control task. When endogenous demands are low, as in the control condition, the tones may serve to stimulate the network, perhaps only transiently, which is why the SART + tone > Control + tone contrast did not show activation of the sustained attention network. The right parietal lobe may play an instrumental role in this interaction between the degree of endogenous demand of the task and the effect of the tone. This region may be active under all SART conditions but controlled differentially via bottom-up or top-down inputs.

The results of this study permit speculation about the degree to which the SART differentially elicits of goal-representation versus arousal, as described by Robertson and Garavan (2004). It has been hypothesized that arousal and sustained attention are separable elements both neuroanatomically and neurochemically, with sustained attention associated with basal forebrain cholinergic inputs and arousal with noradrenergic projections from locus coereleus, mediated by the thalamus (Sarter, Givens, & Bruno, 2001). The role of noradrenalin in arousal has been demonstrated in experiments involving the impact of the noradrenergic agonist, clonidine (Smith & Nutt, 1996). Proposed sites for the interaction of these two networks have included the anterior cingulate (Mottaghy et al., 2006) and the thalamus (Gobbele et al., 2000; Portas et al., 1998; Sarter et al., 2001). Our findings do not address the role of the anterior cingulate as it was not differentially engaged by the SART versus control tasks. Thalamic activity during attentional tasks has been shown to interact with arousal levels. Under low arousal conditions, the thalamus demonstrates greater change in activity than under normal or high arousal conditions, representing the modulation of inputs to prevent the physiological shift into sleep (Gobbele et al., 2000; Portas et al., 1998). We observed attenuation, not amplification, of the thalamic activation with the introduction of tones during the SART. It appears that the SART as implemented in this study elicited the effortful maintenance of the goal state, independent of arousal-inducing stimuli, perhaps because the high arousal state necessary to perform the SART is maintained over the course of the short 60-s block is not influenced by normally arousing stimuli. This does not rule out the existence of a common, right-lateralized, multimodal, cortico-subcortical network mediating sustained attention and arousal (Sturm & Willmes, 2001).

Conclusions

The SART induces endogenous maintenance of vigilant attention with minimal exogenous stimulation. Consistent with prior research and sustained attention theory, performance of this task elicited a right-lateralized network of DLPFC and thalamus. Alerting tones provide stimulation to cue the maintenance of the goal-state, thus reducing the need for top-down attentional control mediated by the right DLPFC. Accordingly, the tones attenuated the vigilant attention network, particularly the right DLPFC. We also found evidence that exogenous stimulation differentially alters the network depending on the degree to which the endogenous system is engaged.

This examination has particular relevance to the study of rehabilitation of vigilant attention following brain damage. Rehabilitation of executive functions often employs bottom-up stimulation that is externally generated or cued. The sensory or perceptual stimulation provided by this type of stimulation is thought to facilitate plastic reorganization of neural circuits at the level of the sensory motor circuits, which in turn facilitates plasticity at the cortical level (Robertson & Murre, 1999). These external prompts often come in the form of auditory or visual reminders and/or prosthetic organizational systems. According to Manly, Hawkins, Evans, Woldt, and Robertson (2002), the value of an external cue to an individual with dysexecutive symptoms lies in its ability to interrupt current activity to initiate a planned action. Manly and colleagues made use of an intermittent alerting tone during the performance of a task known to be sensitive to deficits in executive function. Subjects with severe traumatic brain injury (TBI), who had originally performed more poorly without alerting tones, performed at the level of healthy controls in the presence of alerting tones. Specifically, subjects increased the number of tasks they attempted within the time limit and the time devoted to each task reflected more optimal time allocation. The performance enhancing effect of a content-free random cue has been shown to extend to everyday functioning in a study by Fish and colleagues (2007). Individuals with acquired brain injury, when randomly alerted throughout the day with a text message, were more likely to remember to perform a daily prospective memory task at the allotted time than when uncued. The present study provides some hypotheses as to the mechanisms underlying the beneficial effect of alerting cue, which may disrupt automatic responding in favor of resumption of supervisory control mediated by the right-lateralized sustained attention network, reducing the need for the endogenous control provided by the right prefrontal cortex. Accordingly, a main objective of our behavioral intervention for patients with executive and attentional deficits, Goal Management Training (GMT; Levine et al., 2000; 2007) is to train people to periodically "STOP" what they are doing to review active goal hierarchies and their match to concurrent behavioral output. In a recent study, patients with frontal damage who underwent GMT showed reduced errors and variability of response times on the SART, among other benefits (Levine et al. 2011).

The effect of auditory alerting tones on the network associated with SART performance in individuals with TBI may provide the opportunity to discern the mechanism by which phasic alerting operates during vigilant attention. It is predicted that, in contrast to normal controls, individuals with TBI will not be capable of successful endogenous engagement during the SART and automatic responding will emerge early. The potential for the early emergence of automatic responding will allow an opportunity for the alerting tones to disrupt this automaticity. Disruption may produce a behavioral effect of the tone over the 60-s block and an increase in right prefrontal activation representing resumption of supervisory control. Future fMRI studies of vigilant attention rehabilitation that have the potential to identify the modulatory influence of rehabilitation on neural circuitry following TBI are underway in our laboratories.

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