



EEG source derived salience network coupling supports real-world attention switching

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ABSTRACT

While the brain mechanisms underlying selective attention have been studied in great detail in controlled laboratory settings, it is less clear how these processes function in the context of a real-world self-paced task. Here, we investigated engagement on a real-world computerized task equivalent to a standard academic test that consisted of solving high-school level problems in a self-paced manner. In this task, we used EEG-source derived estimates of effective coupling between brain sources to characterize the neural mechanisms underlying switches of sustained attention from the attentive on-task state to the distracted off-task state. Specifically, since the salience network has been implicated in sustained attention and attention switching, we conducted a hypothesis-driven analysis of effective coupling between the core nodes of the salience network, the anterior insula (AI) and the anterior cingulate cortex (ACC). As per our hypothesis, we found an increase in AI > ACC effective coupling that occurs during the transitions of attention from on-task focused to off-task distracted state. This research may inform the development of future neural function-targeted brain-computer interfaces to enhance sustained attention.

1. Introduction

Cognitive control is a fundamental human ability that allows us to flexibly pay attention to and act upon goal-relevant information, while further suppressing irrelevant distractions (Badre, 2011; Lenartowicz et al., 2010; Luna et al., 2015; Mishra et al., 2013). Likewise, attention is fundamental to cognitive control, and higher cognitive skills such as working memory, learning, and task planning are crucially dependent on it (Fortenbaugh et al., 2017; Gazzaley and Nobre, 2012). Relevant to modern times, sustained attention has been shown to be impacted by the overuse of distracting technologies (Ophir et al., 2009; Ziegler et al., 2015). It has been estimated that U.S. children and youth spend an average of 9 h of their day consuming media in the form of television, internet, email, video games, social networks, and interaction with mobile devices (Common Sense Media, 2015), and that this usage is impacting attention and cognition (Walsh et al., 2020).

Attention and cognitive control have been traditionally studied in tightly controlled laboratory settings. Yet it is important to study attention in real-world contexts that can shed better light on how the brain efficiently processes information in complex situations and environments (Peelen and Kastner, 2014). Hence, in this study, our objective was to investigate the neural dynamics underlying performance on a self-paced, loosely constrained, real-world computerized task. Specifically, we were interested in exploring whether brain connectivity within the salience network, a well-characterized brain network involved in attentional switching (Dosenbach et al., 2006; Menon and Uddin, 2010), can be harnessed using EEG source imaging and if this network is associated with attention switching from on-task to off-task state.

Previous studies have shown that periods of poor sustained attention are characterized by high response time (RT) variability and frequent on-task errors (Esterman et al., 2012; Fortenbaugh et al., 2015). These

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metrics can be obtained on trial-based continuous performance tasks (CPTs) where individuals discriminate task-relevant target information from task-irrelevant non-targets (Conners et al., 2003). Fortenbaugh et al. (2015) acquired data from thousands of individuals across the lifespan on a CPT paradigm and showed that when subjects were attentive (or “on-task”), they exhibited lower RT variability and higher discrimination ability as opposed to when they were distracted (or “off-task”). Moreover, RT variability has been proposed as a behavioral marker for Attention Deficit Disorder (ADD) (Di Martino et al., 2008). Building upon these findings, here we propose to define periods of putative sustained attention and distraction from the variability of keystroke and mouse click events produced by the subject during a real-world task.

In our case, the real-world computerized task was a 1-h task, akin to a standard academic test, consisting of solving high-school level problems, combining self-chosen modules of math, critical reading and comprehension and performed in a self-paced manner. To characterize the fluctuations in brain dynamics that are predictive of distracted behaviors at a millisecond time scale, we continuously monitored brain dynamics with electroencephalography (EEG). In addition to its excellent temporal resolution, EEG is appealing for real-world applications because it is noninvasive and available as a low-cost mobile technology (Bateson et al., 2017; Kumari et al., 2017). Furthermore, we used EEG source imaging rather than sensor activity to localize the brain dynamics around attention switching events because the latter is often confounded by multiple ongoing brain processes and other non-neural (ocular/muscular) signals (Ojeda et al., 2019, 2021).

Although central to our approach, source estimation alone cannot reveal how different brain regions interact dynamically to support attentive and distracted behaviors. To that end, we use source time series to estimate source connectivity. Popular approaches for estimating EEG source connectivity use parametric models based on strong biophysical (David et al., 2006; Kiebel et al., 2009) or statistical (Giraldo et al., 2010; Yamashita et al., 2004) assumptions. These approaches tend to give reasonable results when analyzing event-related brain responses. In this study, we aimed to characterize source connections on an ongoing basis, i.e., not in an event-related design and more akin to steady-state, non-stationary dynamics wherein the assumptions of the parametric models are hard to justify. To circumvent these issues, Lizier et al. (2008) proposed to compute the transfer entropy (TE) between the electrical activity of pairs of brain areas, conditioned on the activity of all the other areas, as a non-parametric measure of their effective (causal) connectivity (EC). Furthermore, it has been shown that TE-based EC is sensitive to ongoing linear and nonlinear brain dynamics (Wibral et al., 2014).

Data-driven characterization of the EC of large-scale cortical networks active in the context of attention switching in a real-world task is not statistically viable in sample sizes used in psychological studies. Hence, we adopted a hypothesis-driven approach focusing on testing whether we can specifically detect salience network activity/connectivity using EEG source imaging during the transitions from on-task to off-task states. The salience network has core regional nodes connecting the anterior insula (AI) and the anterior cingulate cortex (ACC). Based on results from fMRI data, Menon and Uddin (2010) proposed the AI as a hub that mediates the dynamic interactions between different large-scale networks and is implicated in attention switches driven by external and internal events. In their model, Menon and Uddin (2010) postulate that the AI is sensitive to salient external vs. internal events, and that its key function is to identify such events for additional processing, while the coupling with ACC facilitates rapid access to the motor system, thereby triggering behavioral changes when needed. Specifically, the salience network mediates the dynamic switching between the exogenously driven frontoparietal network and the endogenously mediated default mode network. The activity of the salience network is also shown to be more lateralized to the right (rAI) (Menon and Uddin, 2010; Uddin, 2017; Zhang et al., 2019). To the best of our

knowledge, the coupling between the ACC and rAI nodes in the salience network during a real-world computerized task involving self-paced attention switches from externally-driven to internally-driven states, has not been explored. So, to this end, here we hypothesize that within the transition period from on-task to off-task behavior, there may be causal coupling from rAI to ACC.

2. Materials and methods

2.1. Task description and experimental setup

A total of 25 healthy young adult subjects (mean age 23.3 ± 5.7 years; 13 females and 12 males) participated in the study. All participants had completed high school level education and had normal/corrected to normal vision and hearing and did not report any color blindness. All participants were informed of the nature of the experiment and provided written informed consent. The experiment was approved by the IRB committee of the University of California San Diego. Data for 8 of the 25 subjects were excluded in EEG preprocessing, see section 2.3 EEG processing and source estimation section. Hence, all data are presented for a subset 17 healthy adult subjects (subset mean age 24.7 ± 6.6 years; 12 females and 5 males).

The computerized task consisted of solving high-school level problems combining self-chosen modules of math, critical reading and comprehension for 1 h. The task and example questions can be found here: <https://www.prepfactory.com/>. Examples of math questions are, ‘(i) If $3x = 6$, what is x ?; (ii) $x^2 + 3x + 2 = (x+2)^*$ __’ Examples of reading and comprehension questions are, ‘(i) Essays begin with a(n) Introduction/Transition/Conclusion; (ii) What’s the best introduction? Summarily, we concluded .../To begin, it is .../After all, there was .../Accordingly, we tried ...’.

The subjects were instructed to work through the problems at their own pace. All questions were multiple choice only and did not involve answers to any open-ended questions; subjects were encouraged to continuously work on the multiple choice questions in a self-paced manner. Difficulty of questions was automated and adaptive to subject performance such as in a real-world computerized academic test; as the task was an online test, the exact adaptive algorithm was not known to the authors. We did not record individual subject performance scores. As in any real-world computerized task, we allowed them to self-choose when to be on-task and when to be distracted and move away from the task, with the only requirement to move away from the computer during breaks (see Fig. 1).

We measured each subject’s behavior by capturing the keystroke and mouse-click events they generated throughout the task. To this end, we implemented a secure key and mouse logger app that ran in the background. We used the Lab Streaming Layer (LSL (Kothe et al., 2019)) library to co-register the behavioral events with the EEG signal. Each keyboard or mouse event captured received a timestamp by sending to LSL the characters ‘1’ or ‘2’ respectively, thereby obfuscating the exact identity of those events. Participants had to hit the ‘Submit’ button after their response to any question was complete. There was a constant gap between response to a question and the next question. While all keyboard or button press activity was related to responding to the task’s multiple choice questions, we did not record actual performance, hence, correct vs. incorrect responses cannot be distinguished. But this response activity still indicates on-task engagement in that we know that participants were only interacting with this one computerized academic task. They were not allowed to perform any other task, such as web-browsing or checking email were disabled on the computer. Further, participants were explicitly instructed that they can take self-paced breaks from the task, but when they want to do so they must move away from the computer so that there are no more keyboard responses or mouse clicks, ensuring off-task state of response disengagement.

We acquired EEG data at 500 Hz sampling frequency using an LSL-compatible mobile amplifier (Smarting, mBrainTrain, Belgrade,

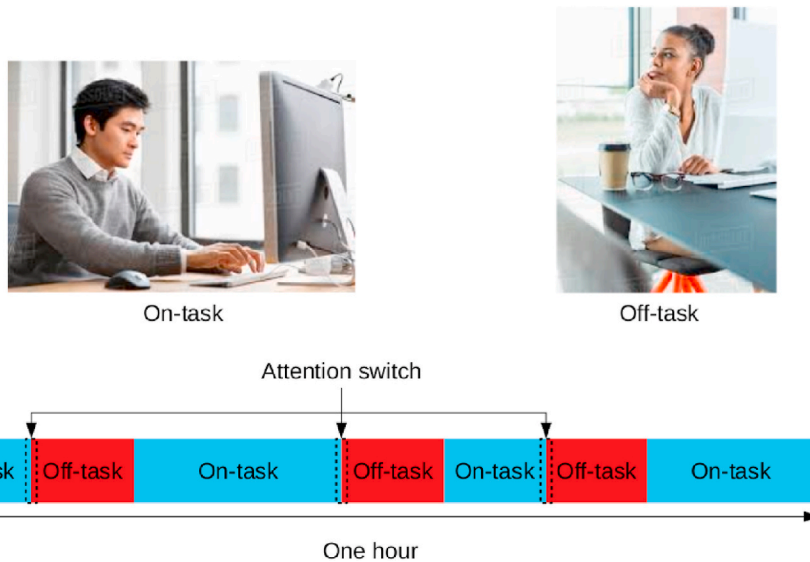


Fig. 1. Self-paced schoolwork-like computerized task. The subjects were instructed to solve problems combining self-chosen modules of math, critical reading and comprehension for 1 h. They were allowed to take as many breaks as they wanted with the only requirement to move away from the computer during breaks. The blue and red blocks represent putative on-task and off-task periods respectively, which we identified using the variability of the subject’s interaction with the computer. We used EEG data 1 s after and before putative transitions from on-task to off-task periods to study the network correlates of attention switching. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Serbia) and a 24-channel electrode montage placed according to the 10/20 system. We recorded event markers and EEG data into an EEGLAB-compatible .xdf file using the LabRecorder app.

2.2. Identification of on-task/off-task epochs

We defined periods of putative sustained attention (on-task) and distraction (off-task) using the variability of keystrokes and mouse click events produced by the subject during the task. The supporting rationale for this comes from prior studies that have shown that response times are consistent during on-task “in the zone” periods while they are more variable during off-task “out of the zone” states (Esterman et al., 2012; Kucyi et al., 2016, 2017). We used a subject-specific 95 percentile of response times (RT) to indicate an off-task switch (see left panel of Fig. 2 and inset histogram); 95 percentile was used as it indicates a significantly longer response time relative to the subject’s usual RT distribution encompassing a period in which the subject was disengaged from the computerized activity, switched off-task and then returned to being on-task; similar rationale has been used to mark off-task switches in

prior studies (Esterman et al., 2012; Kucyi et al., 2016, 2017; Weissman et al., 2006). We defined attention switch events as the last behavioral event before an off-task period. We note that subjects self-chose when to take breaks but were explicitly instructed to move away from the computer during breaks; this was so that the experimenters could observe off-task periods in the response data. In Fig. 2 we show behavior and EEG data from one participant. Fig. 3, on the left shows the total number of attention switch event trials collected for each of 17 subjects (data for the remaining 8 subjects are not shown because they were excluded in EEG preprocessing, see next section). Fig. 3, on the right shows the mean and standard deviation of response times of regular on-task trials compared to post-off-task response trials; the latter are orders of magnitude different than the former and show that on-to off-task disengagement clearly occurred after the attention switch trials.

There were a total of 661 attention switch trials across all subjects that were used for EEG attention switch trial analyses. We had very adequate power for trial based statistics, sample size of 661 trials can detect small Cohen’s d effect sizes ≥ 0.11 of a mean difference from constant at 0.8 power and two-sided alpha of 0.05.

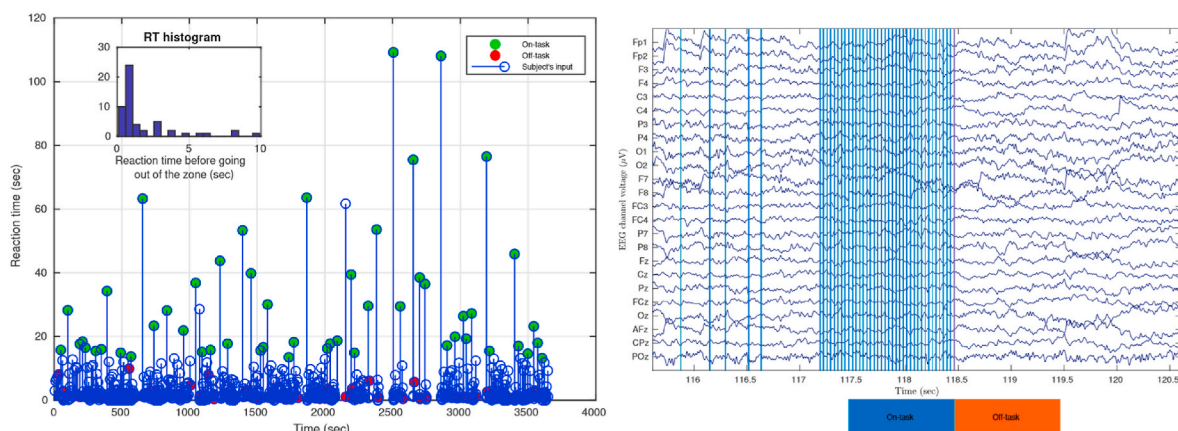


Fig. 2. Identification of attention switch events as the transition from on-task to off-task epochs. **Left:** Behavior of one participant (keystroke and mouse click events) captured by the logger app. The inset histogram shows the distribution of response times (RT)s ranging from responses every second to responses once every 10 s over the course of the hour-long task duration; the 95 percentile of RTs was used to identify when the subject was going out of the attentive zone, i.e., out of active task-engagement into the off-task period. The trials marked with red show the putative end of “on-task” activity, where the next trial has a long RT distribution marking an off-task period. The trials marked with green show the identified end of the “off-task” epochs, i.e., the onset of on-task activity. **Right:** Co-registered behavioral events and EEG signals for an example segment exhibiting an attention switch from on-task state (lots of responses, reflected by blue lines) to an off-task state (no response/engagement on the task). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

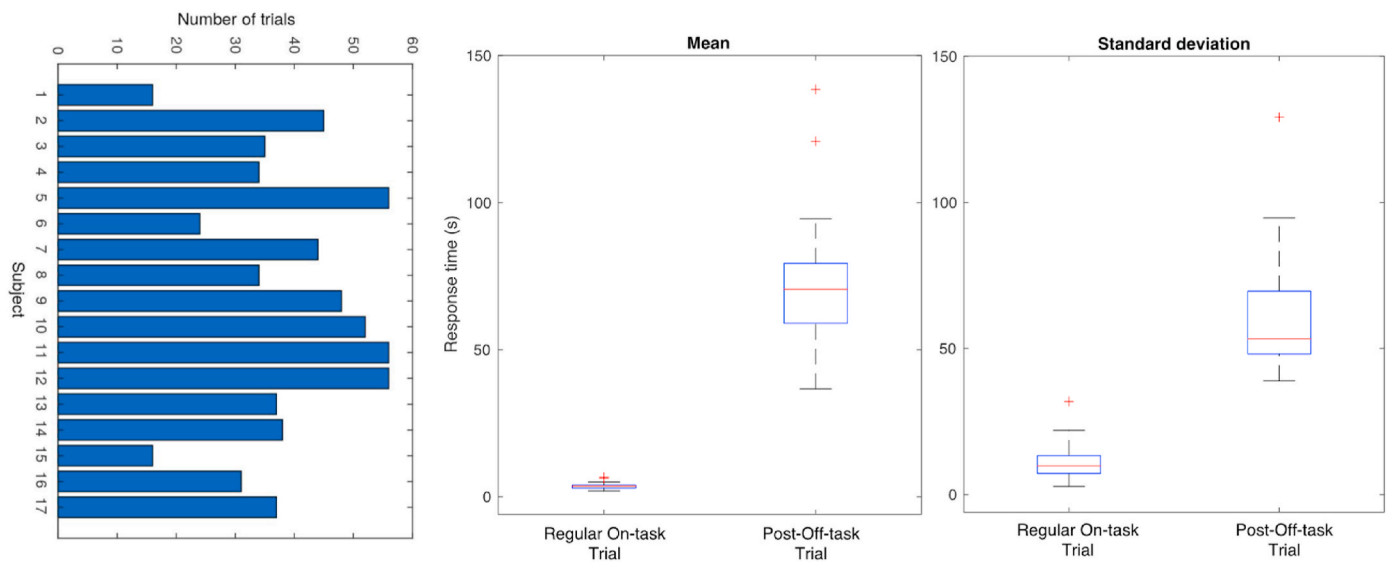


Fig. 3. On left, number of attention switch trials collected for each subject, average 38.8 ± 12 trials per subject, total 661 trials across all subjects. At center and right, box plot of mean and standard deviation of response times for regular on-task trials compared to post-off-task trials, illustrating the orders of magnitude difference between these, showing that on-to off-task disengagement clearly occurred after the attention switch trials. Box plots show median value as red line, the bottom and top edges of the box indicate the 25th and 75th percentiles, respectively, the whiskers extend to the full range of the data, and outliers are plotted individually using the '+' marker symbol. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2.3. EEG processing and source estimation

We processed the EEG data in MATLAB (R2018b The MathWorks, Inc., USA) using the EEGLAB toolbox (Delorme et al., 2011). The pre-processing consisted of a 0.5 Hz–50 Hz band-pass zero-lag FIR (finite impulse response) filter and re-referencing to the common average channel. This choice of filter is convenient for offline analysis as it doesn't shift EEG samples with respect to event markers. We visually inspected the data and removed 8 subjects from the study because they exhibited more than three faulty channel connections throughout the task. Next, we collected trial epochs consisting of 1 s before and after the attention switch events and manually removed those excessively contaminated by artifacts. Artifacts of EOG (electro-oculographic) and EMG (electro-myographic) origin were further cleaned using the Recursive Sparse Bayesian Learning (RSBL) source estimation algorithm (Ojeda et al., 2018, 2021).

RSBL is an online-compatible algorithm in which each EEG sample is localized based on a prediction from the past sample while imposing biologically-inspired sparsity constraints, thereby resulting in compact source maps that evolve smoothly in time. The sparsity constraints are applied to entire regions of interest (ROI) based on the standard 68 brain region Desikan-Killiany (DK) atlas (Desikan et al., 2006) covering the whole cortex. Although this partition is fixed, at any given time, the algorithm determines the contribution of each of the ROIs in a data-driven manner so that cortical regions that are not necessary to explain the scalp topography are down-weighted or even set to zero automatically. This data-driven pruning procedure reduces the effective number of sources considered at any given time as a solution, thereby alleviating the ill-posed nature of the inverse mapping. It has been shown in prior research from our group and others (Balasubramani et al., 2021; Ding and He, 2008; L. Fakhraei et al., 2021; L Fakhraei et al., 2021; Grennan et al., 2021; Stopczynski et al., 2014) that this feature allows obtaining source maps of reasonable accuracy even at low channel densities. It is important to note that although the sparsity constraint is imposed at the ROI level, the actual value of sources within an ROI is not exactly the same, though they can be correlated.

Another important feature of the RSBL algorithm is that artifacts with stereotypical scalp signature can be included in the source model (as artifact sources) and their contribution removed automatically. Here

we modeled EOG and EMG sources based on an artifact dictionary obtained from applying ICA to a large EEG database, see (Ojeda et al., 2018, 2021) for details. Cortical sources were modeled using the four-layer (scalp, outer skull, inner skull, and cortex) Colin-27 head template (Holmes et al., 1998).

The output of the RSBL algorithm was a single-trial EEG source estimates array of 8003 cortical sources by 2 s by trial by subject. Since doing connectivity estimation on an 8003 source space would be impractical, we further collapsed the source dimension into the 68 Desikan-Killiany atlas ROIs. We reduced dimensionality by calculating the ROI power time-series, which was taken as the sum of squares across sources within each ROI.

2.4. Source effective connectivity estimation

We used the ROI power time series to calculate the effective (causal) connectivity between the rAI and rACC ROIs. Effective connectivity was characterized by TE, which we computed on a sliding window of 100 msec with a 50% overlap. To factor out common influences from other ROIs, we conditioned the TE on the activity of the remaining 66 ROIs. We used Kraskov's TE estimator (Kraskov et al., 2004) as implemented in the Java Information Dynamics Toolkit (JIDT) (Lizier, 2014). We also used cross-correlation in MATLAB to assess the possible causal relationship for rAI→ACC connectivity and to quantify its significance.

We note that the primary hypothesis-driven investigation in this study was to assess if rAI – ACC EC is linked with the observed transition in subject's behavior from on-task to off-task periods. For control analyses, during the on-task to off-task period, we also investigated other possibly relevant connections. These included the AI – ACC connectivity on the left side, i.e. lAI – ACC EC to see if observed coupling is specific to the right-lateralized salience network or is bilateral. Apart from the salience network, the frontoparietal network is the other main cognitive control network, which controls exogenously driven and cognitive demanding mental activity (Dosenbach et al., 2006, 2008; Menon and Uddin, 2010). Hence, we also calculated EC for the core nodes of the frontoparietal network, between left dorsolateral prefrontal cortex and left superior parietal cortex (LDLPFC - LSP), and right DLPFC and right SP cortex (RDLPFC - RSP); left/right DLPFC corresponded to the left-/right caudal middle frontal ROIs in the DK atlas.

Further, we also investigated the rAI – ACC EC during the off-task to on-task switch epochs and also during regular response trials that were of duration <95 percentile of RTs; for the latter, 40 regular response trials were randomly selected per subject for a total of 680 regular response trials across 17 subjects in order to approximately match the total number of attention switch trials (661 trials) across all subjects.

3. Results

Here, we followed a hypothesis-driven approach focusing on activity and effective connectivity of the salience network. In particular, we tested whether there is a causal influence of the rAI over the ACC (rAI→ACC) within the 2 s window overlapping the putative attention switch events. If we find this to be the case, it would suggest that salience network connectivity mediated by rAI – ACC is linked with the observed transition in subject's behavior from on-task to off-task periods. We behaviorally characterized the on-task to off-task attention switch events by points at which the participant stopped engaging in the self-paced computerized task, time-locked to subject-specific 95 percentile of RTs.

First, we investigated whether there is rAI/ACC network activity time-locked to the putative attention switch event. In Fig. 4, we show the time series of rAI→ACC connectivity (left) and the power in rAI (right) time-locked to the attention switch event, which is represented by the dashed black vertical trace. The y-axes denote all the trials of all 17 subjects, and the intensity of the colors represent the respective magnitude of the EC and power time series. Here, we observed that there was significant rAI- > ACC effective connectivity during the switch from on-task to off-task epochs. However, there was also considerable jitter within the 1 s window spanning the behavioral switch event.

Given the jitter in the connectivity data around the behavioral attention-switch event, we then time-locked the EC and power data to the maximum of the rAI→ACC connectivity time series for each trial within the same 2 s attention-switch window. This time-locking to max EC more clearly demonstrated the rising and falling strength of the EC and alignment with power in rAI (Fig. 5).

In Fig. 6, we plot the group-level trial average of the rAI→ACC connectivity time series (top) and rAI and ACC power (bottom). The inset equation models the activity of the ACC (y) as a function of rAI activity (x), with terms, t: time relative to rAI→ACC peak connectivity in msec, c: connectivity, and e: noise. We used cross-correlation to assess the possible causal relationship between rAI and ACC. The cross-correlation between these two signals was maximum when the ACC signal was shifted backward 150.532 msec with an R^2 of 0.841,

correlation value for this lag was 0.917 with a p-value of 6.3843e-161, 95% CI [0.903, 0.944). Hence, best fit is observed when ACC activity (y) lags connectivity (c) by 150 msec.

In Fig. 7 we show the specificity of the rAI→ACC peak connectivity within the attention-switch epoch. Here, we analyzed the EC time series statistics (across-trial mean and 5%–95% confidence interval) for other possibly relevant connections: left anterior insula to anterior cingulate cortex (IAI→ACC), left dorsolateral prefrontal cortex to left superior parietal cortex (LDLPFC→LSP), and right dorsolateral prefrontal cortex to right superior parietal cortex (RDLDPFC→RSP). The rationale for investigating these ROI connections is provided in the Methods, Source effective connectivity estimation section. To calculate these EC statistics, we aligned each trial to the putative attention switch event, marked by the peak of the rAI→ACC connectivity within the behavioral attention switch epoch (same procedure as in Figs. 5 and 6). This was done because from a brain network perspective, the peak AI-ACC connectivity marks the putative attention switch from external to internal event salience, while the behavioral attention switch event is simply the last click/button press before the subject goes off-task behaviorally.

In all cases, we failed to detect significant network activity time-locked to the peak of the rAI→ACC event within the time frame analyzed. These analyses serve as controls showing specificity of the rAI→ACC peak connectivity during the attention switch event, undetected in the corresponding left sided network or in the frontoparietal network.

Finally, we also analyzed whether rAI→ACC peak connectivity was observed during the off-task to on-task switch epochs or during regular response trials that were not attention switch trials. In both cases, connectivity was analyzed in the 2 s window around these behavioral events. Given that there may be connectivity jitter (as observed in Fig. 4 for on-task to off-task attention switches), connectivity on each trial was aligned to its peak (same procedure as in Figs. 5 and 6, now applied to off-task to on-task switches and regular response trials). In these two cases, we did not observe any consistent rAI- > ACC EC waveform similar to that observed in Fig. 6 (see Fig. 8). The group-level trial average EC trace in these two cases has the shape of a delta function. The sharp delta function is the consequence of averaging all the maxima i.e. peak connectivity across all trials, so the central point automatically gets reinforced, which is not anything biologically-related. These results show that rAI→ACC peak connectivity is not observed at least within the 2 s epoch around the off-task to on-task switch events, or on regular response trials.

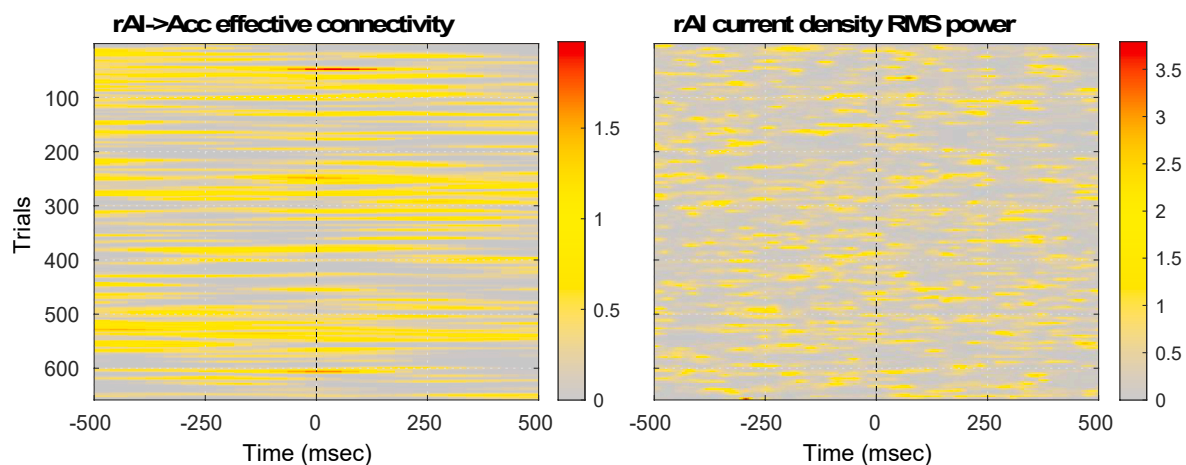


Fig. 4. Salience network connectivity (left) and power (right) dynamics time-locked to the putative attention switch event in each subject, shown for ± 500 msec around the behavioral switch. The y-axes denote all the trials of all subjects and the intensity of the colors represent the respective magnitude of the rAI→ACC connectivity and rAI power time series. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

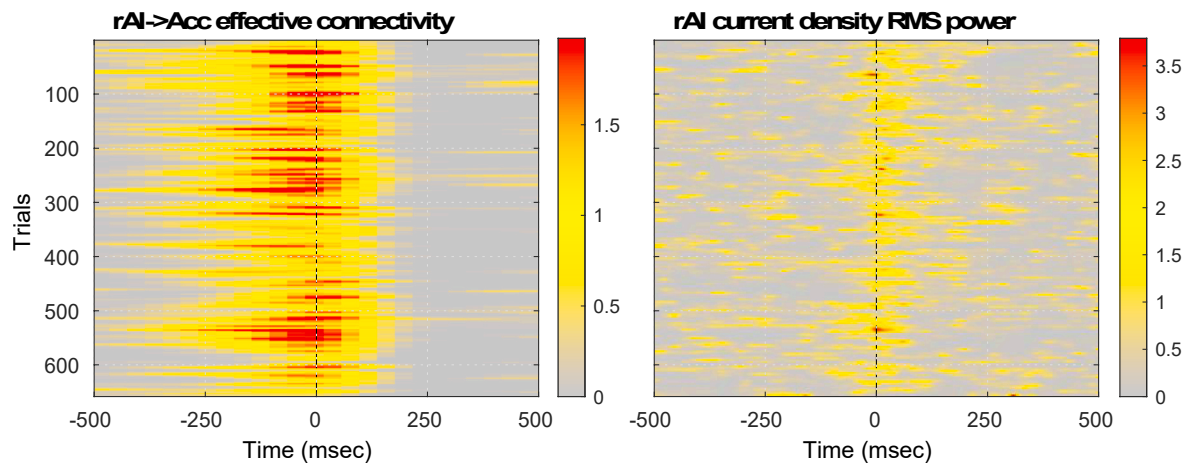


Fig. 5. Saliency network connectivity (left) and power (right) dynamics time-locked to the maximum of rAI→ACC connectivity time series within the attention-switch epoch, shown for ± 500 msec around the max EC. The y-axis denotes all the trials of all subjects and the intensity of the colors represent the respective magnitude of rAI→ACC connectivity and rAI power time series. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

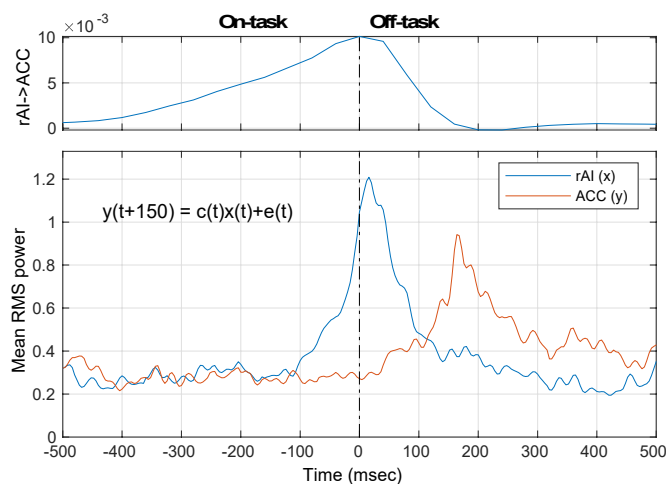


Fig. 6. Group-level trial average of the rAI→ACC connectivity time series (top), aligned to the peak of the EC analyzed within the subject-specific attention switch windows for the on-task to off-task switches, and aligned rAI and ACC power (bottom), shown for ± 500 msec around the max EC.

4. Discussion

Real-world attention naturally switches between on-task focus and off-task distractibility. Yet, common laboratory tasks that study attention with set trial structures for what must be attended versus unattended, do not evaluate such fluctuations of attention that occurs in a self-paced manner. In this study, using EEG source imaging we specifically investigated whether self-paced switches from the on-task to off-task state are associated with activity and connectivity dynamics of the major saliency network nodes, the rAI/ACC.

We first time-locked neurophysiological data to the putative behavioral switch events, when response times fade from active responding to non-responding at the 95 percentile of response times. This analysis (Fig. 4) showed that effective connectivity and power in rAI/ACC can indeed be detected during the transition from on-task to off-task behavior. Yet, we found that effective connectivity observed between rAI/ACC is not perfectly time-locked to the behavioral event (in this case, the keyboard press/mouse click) that we used to identify the transition between states. However, this is not entirely unexpected given the unconstrained nature of the task wherein subjects engaged in solving

high-school level problems at their own pace. Furthermore, our way of identifying the behavioral transition is intrinsically imprecise, i.e., the last keystrokes or clicks in a trial may have been the product of mindless mechanical action. Likewise, the absence of these events does not necessarily imply a sudden switch to a distracted state.

Here, we discovered that during the putative behavioral switch epoch, when we time-lock connectivity and power data to the maximum of the rAI→ACC connectivity, we observe that EC in the saliency network indeed shows a rising to falling transition across all trials and subjects (Fig. 5) within the 2-s vicinity of the behavioral state-transition from on-task to off-task state. These results indicate that information flows from rAI to ACC in the vicinity of the attention switch event, and that this flow was consistent across trials and subjects, thereby, confirming our initial hypothesis. This interpretation is supported even more clearly in Fig. 6, where we observe that the peak of rAI power precedes the peak of ACC power by approximately 150 msec, thus indicating that these two regions are effectively (causally) connected.

Classically, during externally-oriented cognitive tasks, the central-executive network (comprising of the dorsolateral prefrontal cortex and posterior parietal cortex) is active while the default-mode-network regions (medial prefrontal cortex, posterior cingulate cortex) are suppressed (Dosenbach et al., 2006, 2007; Raichle et al., 2001; Sridharan et al., 2008). Sridharan et al. (2008) first showed that anterior insula, and right AI connectivity with ACC in particular, plays a key role in mediating switching between the central executive control network and the default mode network. This work is consistent with others (Dosenbach et al., 2006, 2007) showing that the rAI and ACC comprise a distinct set of brain regions that are involved in task-control across multiple task contexts. rAI seems to play a particularly important role in detecting salient behavioral events (Han et al., 2019). This may include both externally-generated events, as part of the ventral attention network (Eckert et al., 2009) as well as internally-generated/interoceptive cues (Menon and Uddin, 2010). rAI connectivity with ACC seems to be essential for switching between on/off (or external/internal) states and brain networks (Tang et al., 2012). Interestingly, stronger connectivity within this rAI-ACC network has been observed in individuals with better performance on attentional tasks (Touroutoglou et al., 2012). We also recently showed that improvements in sustained attention from a closed-loop digital meditation training protocol are associated with strengthened connectivity in the AI-ACC network (Mishra et al., 2020). Evidence further supports that the rAI-ACC network has clinical relevance, with disruptions in this network observed across a number of clinical populations associated with various

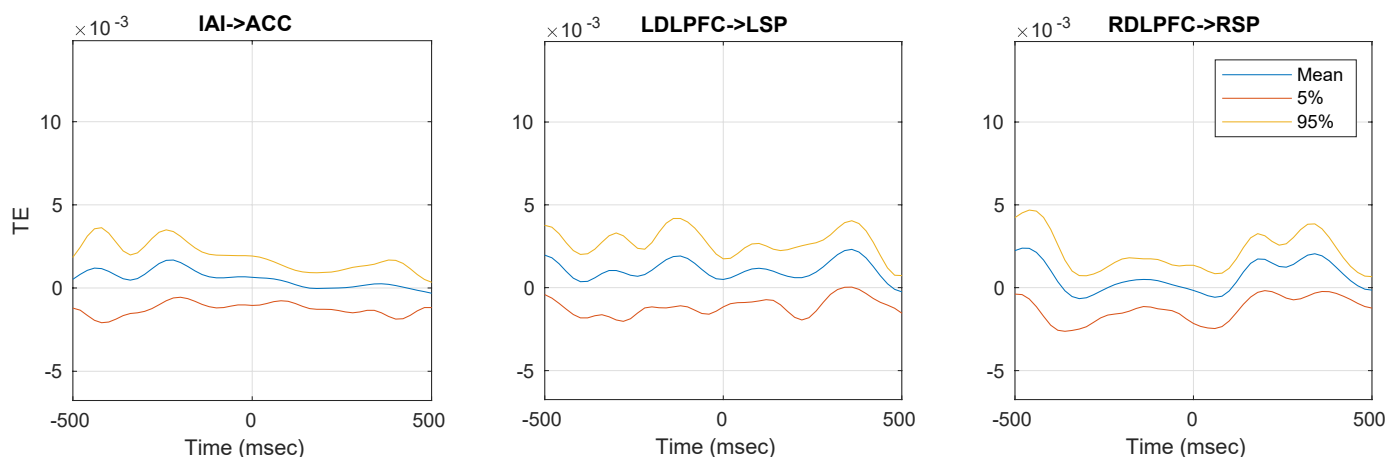


Fig. 7. Group-level trial average and 5%–95% confidence intervals of the effective coupling in other possibly relevant connections, corresponding to the left-side core nodes of the salience network and the left/right frontoparietal network shown aligned to the max EC of the $rAI \rightarrow ACC \pm 500$ msec marking the putative attention switch. No significant peaks are observed in these network connections. TE: Transfer entropy measure of effective coupling; IAI: left Anterior Insula; L/R DLPFC: left/right dorsolateral prefrontal cortex; L/RSP: left/right superior parietal cortex.

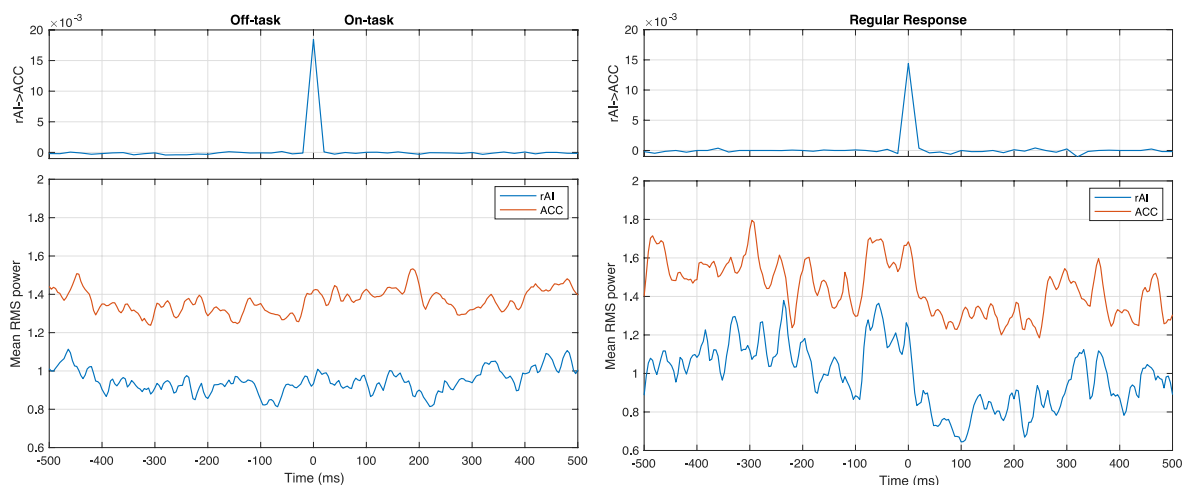


Fig. 8. Group-level trial average of the $rAI \rightarrow ACC$ connectivity time series (top row), aligned to the peak of the EC analyzed within the subject-specific off-task to on-task attention switch windows (left) and regular response trials (right), and corresponding aligned rAI and ACC power (bottom), shown for ± 500 msec around the max EC.

cognitive deficits (Uddin, 2014).

Given the fundamental role that the salience network plays during any cognitive behavior, it is thus not unexpected that we found EC between its core brain regions, even while measuring neural coupling on an unconstrained/naturalistic task. That we were able to observe and measure this EC with scalable EEG source imaging is very promising and also striking. The first direct electrophysiological evidence of connectivity from AI to dorsomedial prefrontal cortex (dmPFC) that encompasses the ACC was shown only recently, using invasive electrodes implanted within AI and dmPFC (Bastin et al., 2017). Recent efforts have estimated functional connectivity within the salience network in source-space (using LORETA) similar to our efforts in this paper (Imperator et al., 2020; Massullo et al., 2020), though these previous studies have measured effective connectivity during resting state, and not dynamically within a task context. We note that here we uniquely show evidence for dynamic $rAI \rightarrow ACC$ coupling in the vicinity of behavioral attention state switches from on-task to off-task state. We further show the specificity of this peak coupling during these behavioral attention switch epochs. Peak connectivity of right $AI \rightarrow ACC$ during the attention switch epochs was not observed to correspond to significant network connectivity for left $AI \rightarrow ACC$ showing the

right-lateralization of the connectivity finding, or any significant connectivity in the left/right frontoparietal brain regions suggesting the salience network specificity. Other researchers have shown causal relationships between salience network and frontoparietal network connectivity in specialized cases such as for divided attention across spatial locations and sensory modalities (Santangelo, 2018), which was not required for our task. Additionally, we showed that the right $AI \rightarrow ACC$ peak coupling was not observed within the 2-s epoch around the off-task to on-task response events, or for regular response trials. The null result for regular response trials is expected, given that attention is not switching between external vs. internal salience during these trials. The null result for off-task to on-task switch trials could be because this putative switch is neurally occurring much earlier than 1-s prior to the behavioral response event, but it was not within our scope to stretch analytics to much longer time windows.

The present work is limited in that we did not resolve the subjects' behavior beyond active keystrokes and mouse-clicks to represent task-engagement, i.e. we do not have a handle on performance accuracy or on difficulty of individual questions, which was automated and represents adaptively increasing cognitive load. Future work is needed to resolve these task performance nuances, especially since the anterior

cingulate node of the salience network is involved in error processing (Botvinick et al., 2004; Hyman et al., 2017; van Veen and Carter, 2002). We also acknowledge the limitation that we do not know the content of the mental activity during the off-task period. Also since the precise timing of the mental switch is uncertain, we may need to use more sophisticated methods to better determine the involvement of the frontoparietal attention network leading to, during, and after the switch, and also stretch the time windows for analyses to find salience network switches from off-to on-task state. For instance, future work may consider using micro-states connectivity analysis (Duc and Lee, 2019) to discover more complex network dynamics at the whole cortical scale.

Taken together with recent EEG-based AI/ACC connectivity studies, our work here suggests that EEG may be a cost-effective approach for measuring effective connectivity within the salience network both at rest and during task contexts. Measuring this at scale (in larger samples, in various psychiatric disorders), may provide a novel platform for identifying links between the functioning of this network and large-scale cognitive and behavioral difficulties. Taken as a whole, the results contribute to the understanding of brain connectivity that supports cognition and behavior. Future closed-loop experiments (Mishra et al., 2016, 2021) will be necessary to show if rAI→ACC network activity is indeed causal to attention switching. For instance, a source imaging-based brain computer interface (BCI) that monitors the rAI→ACC coupling and the power in rAI, and alerts when both increase significantly above threshold, may be useful for averting attention switches to the distracted state.

Credit author statement

AO, VM, DR, JM contributed to conception and design of the study. AO, VM conducted all data collection. AO, MW performed all statistical analyses. AO wrote the first draft of the manuscript. AO, DR, JM contributed to manuscript revision. All authors read and approved the submitted version.

Data availability

Data will be made available on request.

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