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RESEARCH ARTICLE

Time-varying functional connectivity predicts fluctuations in sustained attention in a serial tapping task

Dolly T. Seeburger[1] · **Nan Xu**[2] · **Marcus Ma**[3] · **Sam Larson**[2] · **Christine Godwin**[1] · **Shella D. Keilholz**[2] · **Eric H. Schumacher**[1]

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Abstract

The mechanisms for how large-scale brain networks contribute to sustained attention are unknown. Attention fluctuates from moment to moment, and this continuous change is consistent with dynamic changes in functional connectivity between brain networks involved in the internal and external allocation of attention. In this study, we investigated how brain network activity varied across different levels of attentional focus (i.e., "zones"). Participants performed a finger-tapping task, and guided by previous research, in-the-zone performance or state was identified by low reaction time variability and out-of-the-zone as the inverse. In-the-zone sessions tended to occur earlier in the session than out-of-the-zone blocks. This is unsurprising given the way attention fluctuates over time. Employing a novel method of time-varying functional connectivity, called the quasi-periodic pattern analysis (i.e., reliable, network-level low-frequency fluctuations), we found that the activity between the default mode network (DMN) and task positive network (TPN) is significantly more anti-correlated during in-the-zone states versus out-of-the-zone states. Furthermore, it is the frontoparietal control network (FPCN) switch that differentiates the two zone states. Activity in the dorsal attention network (DAN) and DMN were desynchronized across both zone states. During out-of-the-zone periods, FPCN synchronized with DMN, while during in-the-zone periods, FPCN switched to synchronized with DAN. In contrast, the ventral attention network (VAN) synchronized more closely with DMN during in-the-zone periods compared with out-of-the-zone periods. These findings demonstrate that time-varying functional connectivity of low frequency fluctuations across different brain networks varies with fluctuations in sustained attention or other processes that change over time.

Keywords Sustained attention · Time-varying functional connectivity · Low-frequency fluctuation · Quasi-periodic pattern · Default mode network · Association networks

Introduction

To successfully achieve one's goals and perform optimally in many situations, we must control and sustain our attention. Tasks requiring such attentional control can vary from the mundane, such as listening to a podcast, to highly engaging ones, such as playing basketball. Some think of attention as a light—it is either on or off, but a better metaphor is a flickering candle—even when lit, the flame varies. These fluctuations of attention can occur from moment to moment and across more lengthy time periods (Mackworth, 1948; Dorrian et al., 2004; Esterman et al., 2013; Kucyi et al., 2017; Rosenberg et al., 2020). Sustaining attention is a complex cognitive process that requires both top-down (e.g., knowledge-driven processes

✉ Dolly T. Seeburger
dseeburger3@gatech.edu

✉ Eric H. Schumacher
eschu@gatech.edu

[1] School of Psychology, Georgia Institute of Technology, Atlanta, GA, USA

[2] Department of Biomedical Engineering, Georgia Institute of Technology and Emory University, Atlanta, GA, USA

[3] College of Computing, Georgia Institute of Technology, Atlanta, GA, USA

to bias subject towards signal as opposed to noise) and bottom-up control (e.g., sensory inputs such as the characteristics of the target stimulus) (Sarter et al., 2001).

Brain networks of sustained attention

Scientists have worked to understand the neural mechanisms related to sustained attention (Mesulam, 1990; Dockree et al., 2004; Clayton et al., 2015; Rosenberg et al., 2016). From this work, one thing is clear, attention is not sustained through the activation of isolated brain regions, rather it is mediated by coordinated activity across multiple brain regions (Bressler & Menon, 2010). There are four major brain networks typically implicated in fluctuations in attention control (Yeo et al., 2011). They are the default mode (DMN), dorsal attention (DAN), ventral attention (VAN), and frontoparietal control (FPCN) networks (Fortenbaugh et al., 2017; Esterman & Rothlein, 2019; Zuberer et al., 2021) (Fig. 1).

The DAN is hypothesized to mediate top-down, task-oriented attention (Fox et al., 2005). The core brain regions are the frontal eye fields (FEF), superior parietal lobule (SPL), intraparietal sulcus (IPS), and precentral ventral frontal cortex (PrCv). The FPCN is believed to mediate executive control (Corbetta & Shulman, 2002; Vincent et al., 2008) and consists of the posterior dorsolateral prefrontal cortex (pDLPFC), the rostrolateral prefrontal cortex (RLPFC), anterior inferior parietal lobule (aIPL), posterior dorsomedial prefrontal cortex (pDMPFC), and middle temporal gyrus (MTG) (Yeo et al., 2011). Combined, these two networks are sometimes called the task-positive network (TPN) (Petersen & Posner, 2012).

The VAN is said to play a role in monitoring salient inputs. It is sometimes referred to as the salience or ventral salience network (Seeley et al., 2007; Menon & Uddin, 2010). A meta-analysis found that the VAN is strongly associated with oddball effects, leading to the conclusion that this network is crucial in alerting (Kim, 2014). The main cortical brain regions in the VAN are the anterior insula (AI) and dorsal anterior cingulate cortex (dACC). The model proposed by Bressler & Menon (2010) suggests that the antagonism between the DMN and DAN is mediated by the VAN. Further research has shown that the VAN works with FPCN and can couple with either DMN or DAN depending on whether one is attending to internally or externally directed goals, respectively (Vossel et al., 2014; Beaty et al., 2015).

Another association brain network implicated in task performance is the DMN. The core DMN brain regions include the medial prefrontal cortex (mPFC), the posterior cingulate cortex (PCC), the precuneus, as well as the right frontal and left occipital regions. This network is most active during activities related to internal processes, such as introspection, emotion perception, beliefs and intention, theory of mind, and mentalizing (Gusnard et al., 2001; Iacoboni et al., 2004; D'Argembeau et al., 2005; Spreng et al., 2009; Spreng & Grady, 2010). Furthermore, the DMN has frequently been found to deactivate during task performance and works in an antagonistic way with the TPN (Fox et al., 2005). However, there is some disagreement in the literature on exactly how DMN activity supports behavior. Some studies suggest that the DMN is detrimental to performance (Weissman et al., 2006; Boly et al., 2007; Eichele et al., 2008; Christoff et al., 2016; Godwin et al., 2023), whereas others claim that intermediate levels of DMN activity can improve outcomes (Gilbert et al., 2006; Hahn et al., 2007; Mason et al., 2007; Sadaghiani et al., 2009).

Reaction time variability as a behavioral correlate of sustained attention

There may be many reasons for this ambiguity in the literature. A difficulty in studying sustained attention is finding a behavioral correlate to fluctuations of attention at shorter timescales. Classical vigilance tasks involve recognizing

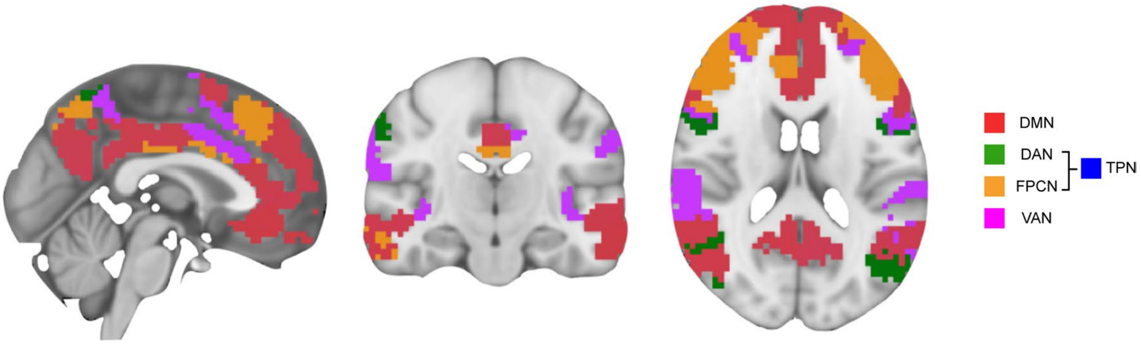

Fig. 1 Four major networks of the brain involved in attention. Default mode network (DMN), dorsal attention network (DAN), and frontoparietal control network (FPCN) combined is the task-positive network (TPN) (Petersen & Posner, 2012), and ventral attention network (VAN) (Schaefer et al., 2018)

that a stimulus changes intermittently. This ability may fluctuate over minutes to hours (Mackworth, 1948; Dorrian et al., 2004), but given the low rate of required overt responses, some tasks cannot differentiate fluctuations that take place on faster timescales. More continuous tasks have been successfully used to measure attention at these timescales. For example, Conner's CPT-II (Conners, 2000), gradCPT, a gradual change detection task (Rosenberg et al., 2013; Esterman et al., 2013), sustained attention to response task (SART) (Robertson et al., 1997), paced finger tapping task (Seli et al., 2013), self-paced finger tapping task (Kucyi et al., 2017), and breath counting task (Levinson et al., 2014) all have a high temporal sensitivity.

While behavioral measures, such as error rates, have been proposed to be good objective correlates to attention (Manly et al., 2000), other researchers (Esterman et al., 2013; Yamashita et al., 2021) have suggested that reaction time (RT) variability is a better trial-to-trial measure for studying fluctuating attentional states within an individual. Unusually slow RTs may indicate a lack of readiness or reduced attention to a task (Cheyne et al., 2009). Whereas abnormally fast RTs may indicate premature or routinized responding and have been associated with failures of attentional control and response inhibition (Weissman et al., 2006). Other studies (Bastian & Sackur, 2013; Seli et al., 2013) also have shown that deviations in performance variability is associated with mind wandering. In a recent experiment triangulating subjective experience with objective measures, Godwin & colleagues (2023) found that the highest average variance RT was reported when subjects subjectively judged themselves "off-task" and the lowest variance RT was reported when they thought they were "on-task." Furthermore, intraindividual variability in RT has been linked to impairments of attention and executive function seen in attention-deficit hyperactivity disorder (Tamm et al., 2012), which supports the idea that erratic responding is related to greater deficits in attention. These results support the claim that RT variability can be used as an indicator of the level of sustained attention to a task.

Esterman & colleagues (2013) proposed categorizing behavior into two zone states based on RT variability. The first state, postulated to capture focused attention across time, is the in-the-zone state. It reflects optimal engagement with a task and is marked by stable responding, skillfulness, or mastery, which culminates in the perception of being in control. Esterman & colleagues speculate that in-the-zone captures the phenomenon *flow* (i.e., the engaged activity of capably performing a difficult task; Csikszentmihalyi, 2009). The second state, on the other hand, captures when attention wanes and we often feel out-of-the-zone. Being out-of-the-zone or colloquially, "zoned out," is marked by an unstable performance that can lead to more errors. Suboptimal experiences can be on either extreme from underengagement, capturing phenomena, such as boredom and mind wandering, to overengagement, such as hyperattentiveness as a result of overthinking (Esterman et al., 2014). Other reasons for feeling out-of-the-zone can be attributed to the lack of arousal or drowsiness, which has a downstream effect on behavior (Godwin et al., 2023).

Esterman & colleagues (2013) found that sustained in-the-zone periods were associated with moderate DMN activity. Moreover, while in-the-zone, higher activity of DMN precedes and persists after an incorrect response, indicating that as automatic responding sets in, there may be a tendency to mind wander and in turn cause a lapse in attention. Conversely, when participants were out-of-the-zone, there was less activity in DMN and higher activity in DAN. They posit that optimal performance may rely not just on activity in one network, but it might involve balancing activity between DMN and DAN. In the current study, we adopt the categorization of zone states to demarcate sustained attention performance as defined by Esterman & colleagues by RT variability.

Time-varying functional connectivity to capture attention fluctuations

Early studies of sustained attention using fMRI measured brain connectivity by computing regional correlations across the duration of the scan, which can last from seconds to minutes (Adler et al., 2001; Lawrence et al., 2003; Strakowski et al., 2004). This assumption of stationarity is problematic given the fluctuating nature of attention. Additionally, researchers have found spatiotemporal activity and connectivity changes across seconds within a scan (Chang & Glover, 2010; Majeed et al., 2011; Liu & Duyn, 2013). Studies suggest that the time-varying properties of functional connectivity between regions can possibly produce different results depending on the timescale used to investigate the activity of the regions (Handwerker et al., 2012; Hutchison et al., 2013; Allen et al., 2014). These differences may explain the contradictory claims that DMN and DAN can both support and be detrimental to performance. Esterman & colleagues (2013) posit that a limitation may arise from looking at brain activation in isolation which does not provide a full neural mechanistic explanation for fluctuations of attention. Consequently, Kucyi & colleagues (2017) employed a time-varying measure of functional connectivity that tracks the variance of RT and the associated brain regions. They found that increased moment-to-moment RT variance correlates with increased functional connectivity between the DMN and VAN (also known as the salience network [SN] in their study).

Our study utilizes a different time-varying functional connectivity approach to bring clarity to the relationship between the synchronization of attention networks and how they relate to sustained attention.

Framework of sustained attention

Kucyi & colleagues (2017) proposed a framework for sustained attention (shown in Fig. 6a). During in-the-zone periods of sustained attention, they reported regional activation of the DMN and lower activity in the DAN and the VAN/SN. While out-of-the-zone periods were associated with lower activity of DMN and higher activity in the DAN and VAN. These results concur with the findings by Esterman & colleagues (2013). Furthermore, in-the-zone periods were marked by lower inter-regional functional connectivity within the regions of the DMN, and lower connectivity between DMN and salience network. While on the inverse, out-of-the-zone periods correlated with higher connectivity within DMN, and higher connectivity between DMN and salience.

Their framework focused on only the relationship between DMN and VAN, and the results came from analyzing the higher BOLD signal frequency (high-pass temporal filter of 0.01 Hz). To add to the current understanding of the brain mechanisms of sustained attention, our study investigated the inter-regional relationship between the attention networks (DAN, FPCN, and VAN) and how they relate with the DMN on the low frequency. To do so, we employed a novel method that captures the repeating low-frequency fluctuations between the brain networks called the quasi-periodic pattern (QPP) analysis.

Repeating low-frequency fluctuations in the brain: the quasi-periodic pattern

In 1995, Biswal & colleagues noticed that there are neuronal fluctuations of <0.01 Hz with temporal coherence across the hemispheres of the brain and are larger in magnitude in the grey matter than the white matter (Biswal et al., 1995). Consequently, this led many groups to interrogate these low-frequency fluctuations with varying methods on a variety of modalities. For example, there have been studies using electroencephalography (EEG) (Grooms et al., 2017; Leopold et al., 2003; Helfrich et al., 2018), local field potentials (LFPs) (Pan et al., 2013), and fMRI (Majeed et al., 2011; Thompson et al., 2014). Using EEG, researchers found that periodicity exists in the low-frequency fluctuations (Valera et al., 1981; VanRullen & Koch, 2003) that may be linked to perception mainly through feedforward connections from sensory to association areas (Bastos et al., 2015, Spyropoulos et al., 2018). In 2018, Helfrich & colleagues supported this idea that the neural mechanism of sustained attention is rhythmic by showing attention-related theta-band (~4 Hz) oscillations of frontal and parietal cortical areas (regions of the FPCN) using intracranial EEG. Using fMRI, Majeed & colleagues (2011) reported spontaneous periodic repeating low-frequency fluctuations that lasts approximately 20 s in humans. They called this the quasi-periodic pattern (QPP).

The QPP signal is marked by a reliably observed pattern of anticorrelation between the BOLD signal of the DMN and the TPN. The QPP measures dynamic changes in connectivity across a longer timescale (~20 s) compared with other dynamic measure, such as coactivation patterns (Chen et al., 2015; Liu et al., 2018; Smith et al., 2018). Moreover, the QPP retains information of temporal ordering of the BOLD signal within the time window. Since then, the QPP has been found in humans during resting-state and task scans (Majeed et al., 2011; Thompson et al., 2013; Abbas et al., 2019a) in rats (Majeed et al., 2009, 2011; Thompson et al., 2014), mice (Belloy et al., 2018), and macaques (Abbas et al., 2016) while awake and anesthetized. Germane to our study, in 2013, Thompson & colleagues discovered that faster responses on a psychomotor vigilance task were associated with higher anticorrelation of the QPPs in the DMN and the TPN than slower responses. Similar differences were found in an ADHD group where the DMN and TPN was less anticorrelated compared with the control group (Abbas et al., 2019b). Others also have reported comparable dynamic relationships within and between the DMN and DAN and salience (VAN) networks (Raccah et al., 2018; Kucyi et al., 2020).

Neural synchrony in the infraslow timescale may facilitate the coordination and organization of information processing in the brain (Buzsaki & Draguhn, 2004; Fox et al., 2005) and is likely related to arousal (Raut et al., 2021). Methods, such as the QPP, may capture the brain's global state of synchrony during periods of sustained attention and relatedly arousal. To investigate this, we used data collected by Godwin & colleagues (2023) to study mind wandering. While they analyzed the static functional connectivity of off-task thoughts based on subjective reporting, we looked at a measure of dynamic functional connectivity (i.e., the QPP) varied with changes in sustained attention. We posit that the QPP will exhibit greater segregation between the DMN and TPN during periods of low RT variability, indicative of sustained attention (viz., in-the-zone). This is in contrasts with times of high RT variability (viz., out-of-the-zone) corresponding to periods of lapses in attention. This hypothesis is grounded in previous findings demonstrating QPP differences related to both attentional capabilities (Abbas et al., 2019b) and performance variations (Thompson et al., 2013).

Method

Participants

Using the dataset from Godwin & colleagues (2023), there were 31 participants with fMRI scans and behavioral data. Their age ranged from 18 to 23 years (M = 20, standard deviation [SD] = 1.6). They were right-handed, had normal or corrected-to-normal vision, and did not report previous neurological or psychiatric conditions. To avoid including participants who may have fallen asleep, participants that tapped on less than 90% of the trials were excluded. This excluded two participants, leaving 29 participants (15 males, 13 females, and 1 gender unidentified; average age: 19.6 ± 1.6 years) in this analysis.

Task and procedure

Participants performed a metronome response task (MRT) (Seli et al. 2013). They were instructed to tap along to a metronome tone as synchronously as possible. The task was organized into a series of blocks of tapping. These tapping blocks consisted of a 450-Hz tone presented for 75 ms. A 1300 ms of silence preceded each tone. In total, the metronome sounded at a rate of approximately 0.77 Hz (one tone per 1300 ms) (Fig. 2). A baseline fixation cross of 2–4 s preceded each tap period, which remained on screen during the duration of the taps. There were five runs and 15 tapping blocks in each run which were made up of six tapping blocks of 16 s, three blocks of 20 s, two blocks of 24 s, two blocks of 28 s, one block of 32 s, and one block of 36 s (run time = 10 min 33 s). The order of the blocks was randomized across runs.

Participants tapped by pressing a button with their right index finger. After each tap period ended, thought probes were shown on the screen to measure their subjective rating of on-task and off-task. If participants selected the off-task option, they were then presented with two additional prompts to further address the nature of off-task thoughts. See Godwin & colleagues (2023) for the results of the subjective analysis.

fMRI design

Imaging was conducted on a Siemens 3T Trio MRI scanner at the GSU/GT Center for Advanced Brain Imaging. At the start, a T1-weighted MPRAGE anatomical scan was collected with the following acquisition parameters: FoV = 256 mm; 176 slices; 1.0 x 1.0 x 1.0 mm^3 voxels; flip angle = 9°, TE = 3.98 ms; TR = 2250 ms; and TI = 850 ms. Next, participants completed the experiment consisted of five functional runs, each for a total duration of approximately 10 min and 33 s of 15 blocks of tapping and the respective thought probe periods that lasted around 20 s each. In particular, functional T2*-weighted echoplanar scans were collected during the runs with the following acquisition parameters: FoV = 204 mm; slices = 37; 3.0 x 3.0 x 3.0 mm^3 voxels; interleaved slice acquisition; gap = 0.5 mm; flip angle = 90°; TE = 30 ms; and TR = 2000 ms.

Behavioral data analysis

Tapping reaction time (RT) were analyzed by using Seli and colleague's method (2013) of calculating rhythmic RTs, which is the difference in the time of a participant's pressing of the button response box time-locked to the

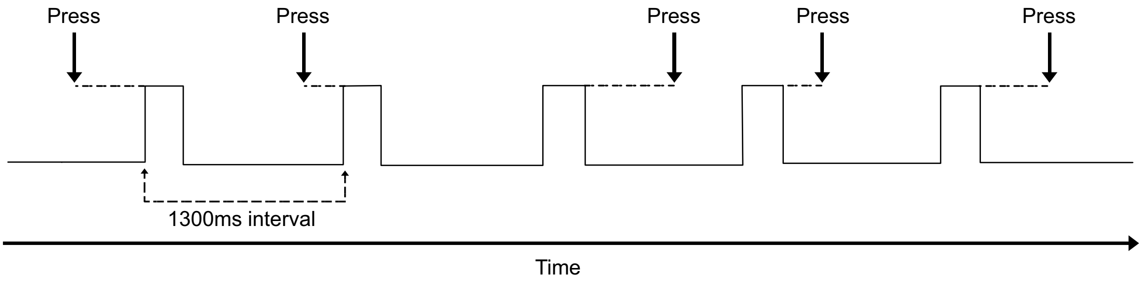

Fig. 2 Serial tapping task. Participants were instructed to tap along to a metronome tone as synchronously as possible. Each tone was separated by 1300 ms

metronome's tone onset time. Within each run, RT variability for each block variance was calculated by taking the average variance of each rhythmic RT within the block. Then, a natural logarithm transformation was applied to adjust for the right-skewed distribution of rhythmic RT. Finally, to get the run RT variability, we averaged the log-transformed RT variability of all 15 tapping blocks. Within each subject, the runs were rank-ordered from highest to lowest RT variability. The run with the highest variability was labeled *out-of-the-zone* and the run with the lowest variability was labeled *in-the-zone* based on the categorization of Esterman & colleagues (2013). Only these two extreme variability runs out of the five runs collected were analyzed in our study.

fMRI data preprocessing

Data preprocessing was performed by using the configurable pipeline for the analysis of connectomes (C-PAC) (Craddock et al., 2013). This pipeline uses FMRIB software library (FSL) version 5.0 (Smith et al., 2004; Woolrich et al., 2009; Graham et al., 2016) and the analysis of functional neuroImages (AFNI) software (Cox, 1996).

Anatomical scans (T1 images) were bias field corrected, skull stripped, and registered to the 2-mm Montreal Neurological Institute (MNI) atlas (Jenkinson & Smith, 2001; Jenkinson et al., 2002). Functional scans (EPI sequences) were slice-time and distortion corrected, masked, and motion corrected. Nuisance signal regression was conducted by using the default settings of the C-PAC pipeline. Spatial smoothing was done by using a Gaussian kernel with a full width at half maximum of 4 mm. Temporal filtering was set at a bandpass between 0.01 Hz and 0.1Hz. Global signal was regressed after. Next, quadratic detrending was applied. To minimize the confound of head motion on our analysis, we followed the guidelines (Yousefi et al., 2018) and found that all our functional scans fell within the acceptable ranges measured by framewise displacement. Twenty-five of 29 of the in-the-zone runs and 24 of 29 of the out-of-the-zone runs were classified as "low movers" and were included in the analysis. Further classification of temporal ratio within those nine scans found that the spikes were less than 40% per run. Hence these "low-moderate movers" also were included in the analysis. All voxel time courses were z-scored to standardize the data for group-level analysis. The preprocessed images were then divided into the 7-network parcellation by Schaefer et al. (2018), which includes 400 defined regions of interest (ROI). The C-PAC pipeline is openly available at www.nitrc.org.

Quasi-periodic pattern template acquisition and analysis

A pattern-finding algorithm originally described by Majeed et al. (2011) and further refined (Yousefi & Keilholz, 2021; Xu et al., 2023) is applied separately to the concatenated brain sequences of all participant's in-the-zone runs (n = 29) and out-of-the-zone runs (n = 29). Each run was approximately 10 min 33 s (volumes = 310, TR = 2000 ms). The QPP detection algorithm can be summarized in these steps. First, it selects an initial spatiotemporal brain pattern of 20 s (starting at timepoint = 1) of the concatenated brain sequence (volumes = 8990 volumes). Second, it uses a sliding window correlation to iteratively search across the run for spatiotemporal patterns where the BOLD signal correlates, at a threshold of local maxima of r = 0.2, with the initial pattern. Third, as the correlating patterns are identified, they are averaged into the original pattern (updating the pattern as the search progresses). This process continues until the end of the concatenated brain scans. Steps 1–4 are repeated for all starting timepoints excluding the last 20 s (10 volumes) within each participant. Lastly, the number of instances where the BOLD signal correlates above threshold for each different spatiotemporal pattern are summed and ranked. The pattern with the highest sum (occurrence) is selected as the representative QPP for each zone state. In this way, the algorithm identifies the most commonly repeating pattern of network activity across both zone states (viz., in-the-zone and out-of-the-zone) for each subject. A process flowchart can be found in (Yousefi & Keilholz, 2021; Figs. S2–S3) and the code for QPP analysis is openly available at https://github.com/GT-EmoryMINDlab/QPPLab.

Statistical analysis

The mean QPP for each zone state is the most commonly occurring pattern of synchronization across the brain networks. Within each zone state, we compare the DMN time course with the other networks of interest (TPN, DAN, FPCN, and VAN), by applying a standard Pearson's correlation. Within individual QPPs are averaged from the instances within a participant's scan where the BOLD signal correlated with the mean QPP for the zone state. Similarly, a standard Pearson's correlation was used to compare DMN to the other networks. The within individual QPPs are visualized as histograms of the distributions of correlations between DMN and the other networks (Figs. 3 and 4). To make statistical comparisons between the within individual QPPs of each zone state, we first transformed the within individual QPP Pearson's correlation using the Fisher's r-to-z transformation. Then, we ran a two samples t-test on the r-to-z transformed correlations. To understand whether the networks are similar between the zone states, we compared each network from the mean QPP to its zone state counterpart with a standard Pearson's correlation (Fig. 5).

Results

DMN and TPN correlation comparison within zone states

The resulting mean QPP template in the DMN and TPN representing each zone state is shown in (Fig. 3). For in-the-zone, the DMN negatively correlated with TPN ($r = -0.89$), whereas in out-of-the-zone, these regions positively correlate ($r = 0.58$). When probing the differences in the distribution of DMN to TPN r-to-z transformed correlations within individual QPPs, it showed that the samples were significantly different from each other, $t(56) = -4.22$, $p < .001$, 95% confidence internal (CI) [−0.87, −0.31], in-the-zone (M = −0.45, SD = 0.53), out-of-the-zone (M = 0.14, SD = 0.53).

DMN's relationship with DAN, FPCN, and VAN within zone states

To further interrogate the relationship of other networks hypothesized to play a key role in sustained attention, we plotted the mean QPP template's subnetworks of TPN (DAN and FPCN) and the VAN against DMN. As shown in Fig. 4a, DAN activity was unaffected by zone state, negatively correlating with DMN in both in-the-zone with a mean correlation of ($r = -0.97$) and out-of-the-zone ($r = -0.91$). It also is clear that the distributions of the r-to-z transformed correlations do not differ between the within individual QPPs of each zone state, $t(56) = 0.84$, $p > .05$, 95% CI [−0.16, 0.38], in-the-zone (M = −0.80, SD = 0.46), out-of-the-zone (M = −0.92, SD = 0.56).

On the other hand, the FPCN decoupled from DMN while in-the-zone ($r = -0.47$) and is positively correlated with DMN while subjects were out-of-the-zone ($r = 0.97$) (Fig. 4b), and the two samples were significantly different $t(56) = -5.61$, $p < .001$, 95% CI [−1.30, −0.62], in-the-zone (M = 0.13, SD = 0.69), out-of-the-zone (M = 1.09, SD = 0.61). VAN showed the opposite pattern to FPCN. It was positively correlated with DMN during in-the-zone ($r = 0.45$) and negatively correlated with DMN during out-of-the-zone ($r = -0.93$) (Fig. 4c). Both distributions of the r-to-z transformed correlations also were significantly different $t(56) = 7.18$, $p < .001$, 95% CI [0.69, 1.23], in-the-zone

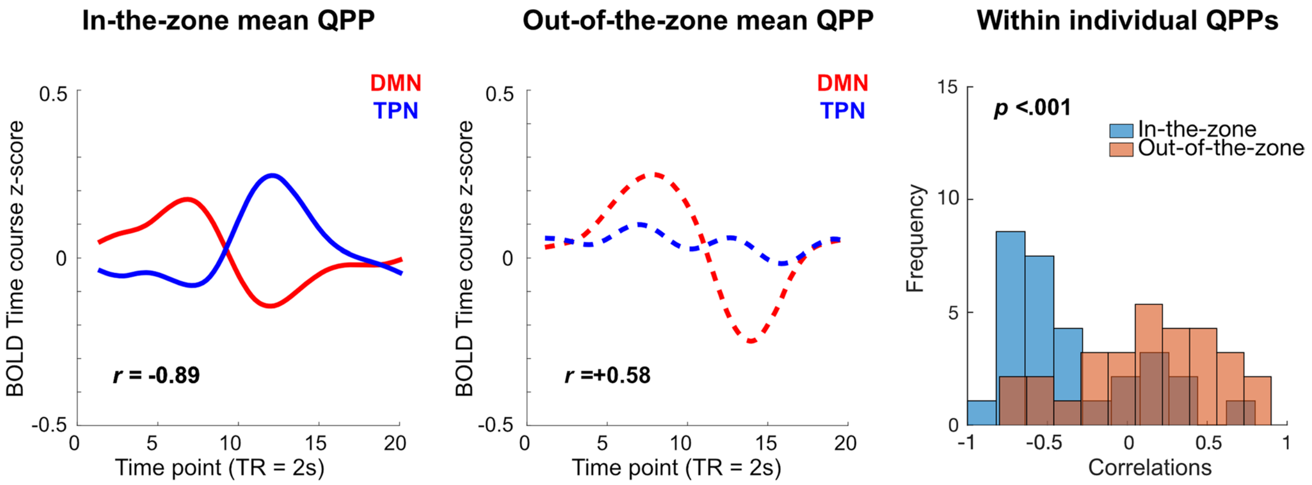

Fig. 3 TPN synchronization with DMN. (Left and center) Mean QPP of DMN and TPN for both zone states. (Right) Histogram of the within individual QPPs of DMN and TPN correlations for both zone states ($p < .001$)

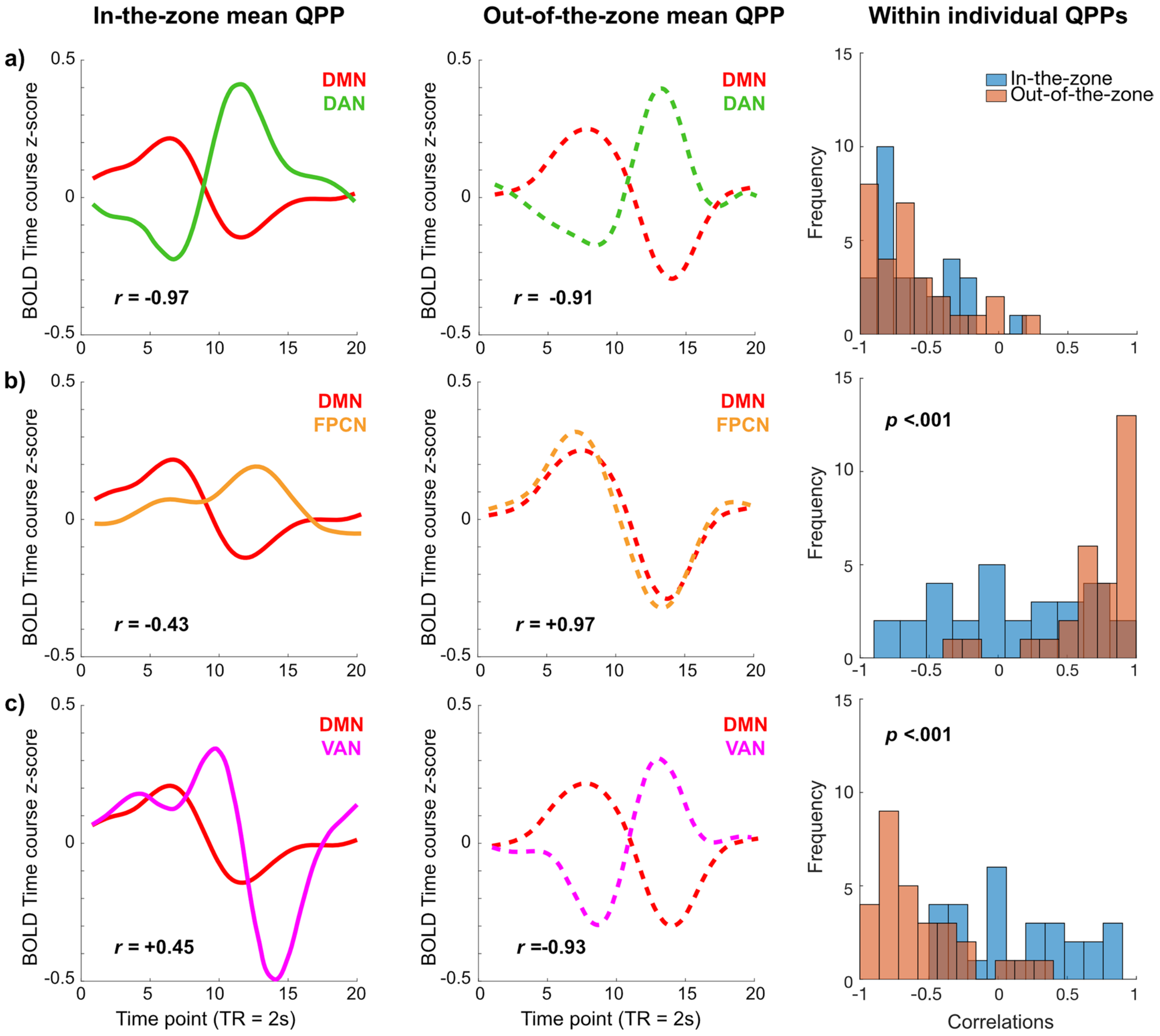

Fig. 4 Attention networks synchronization with DMN. (Left and center) Mean QPPs of DMN and DAN (**a**) DMN and FPCN (**b**), DMN and VAN (**c**) for both zone states. (Right) Histograms of the within individual QPPs of DMN and DAN (**a**) showed no difference, whereas DMN and FPCN (**b**), DMN and VAN (**c**) showed significant differences ($p < .001$)

(M = 0.19, SD = 0.52), out-of-the-zone (M = −0.77, SD = 0.50).

Comparison of networks across zone states

To identify which networks differentiated the zone states, we compared each network from the mean QPP template to its zone state counterpart (Fig. 5). The DMN was positively correlated between zones, $r = 0.72$. Similarly, DAN was positively correlated, $r = 0.76$. Whereas activity in FPCN during each zone state was negatively correlated, $r = -0.45$. Lastly, the VAN was highly negatively correlated across conditions, $r = -0.83$.

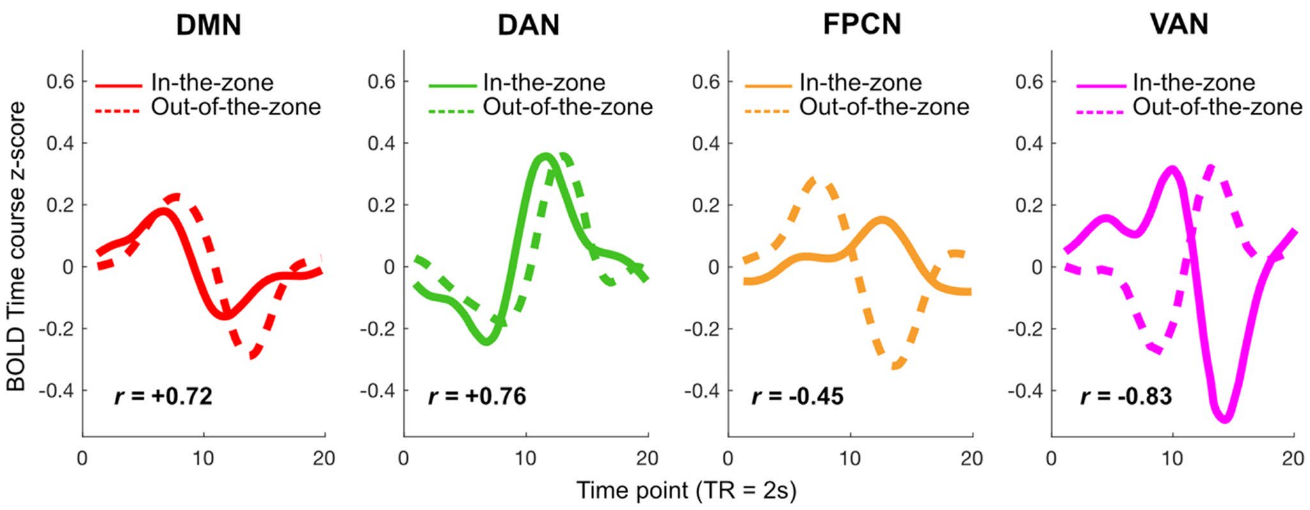

Fig. 5 Networks compared across zone states. Both DMN and DAN were positively correlated. The FPCN were negatively correlated. The VAN reported the most difference between zone states

Discussion

In this study, we investigated the relationship between brain networks during moments of more, or less engaged sustained attention. Previous research has shown changes in network relationships relating to sustained attention (Esterman et al., 2013; Kucyi et al., 2017). The current study investigated dynamic changes in network connectivity as attention fluctuates. Specifically, we interrogated low-frequency fluctuations, commonly called QPPs, and hypothesized that QPP relationship between DMN and TPN would differ in in-the-zone and out-of-the-zone performance. This hypothesis was supported (Fig. 3). Additionally, we discovered that the change in relationship was primarily the result of the FPCN (Figs. 4b and 5). We found that the VAN in the QPP also varied across attentional zone states (Figs. 4c and 5).

Sustained attention and brain network connectivity

As predicted, within the QPP, the time course between the DMN and TPN during the in-the-zone condition was significantly more anticorrelated than out-of-the-zone's (Fig. 5). That is, more successful sustained attention was associated with more segregation between these networks. This result complements previous research showing that faster response is associated with higher anticorrelation between DMN and TPN (Thompson et al., 2013). Moreover, Abbas & colleagues (2019b) found a similar relationship in ADHD patients. Specifically, they found that the QPP was more segregated in healthy controls than in patients with a chronic impairment of sustained attention. Taken together, the results suggest that the decoupling of the two networks in the low-frequency brain activity is correlated with better sustained attention. This antagonistic relationship between the networks also has been reported in many studies using static connectivity (Kelley et al., 2008; Hoekzema et al., 2014; Magnuson et al., 2015).

We found that the subnetworks within TPN were differentially related to zone states. Changes in FPCN connectivity across conditions was responsible for the DMN-TPN differences between in-the-zone and out-of-the-zone states, whereas DAN and DMN's relationship remained similar across the states (Figs. 4a, b). Further comparison of the FPCN from each zone state showed that they were significantly negatively correlated with each other (Fig. 5). That is, FPCN changes across zone states. Previous research has shown that DAN and FPCN have distinctive relationships with DMN (Yousefi & Keilholz, 2021), but this is the first demonstration that these relationships are related to sustained attention and suggests that the FPCN plays an import role in engaged attention—at least in this task.

Theorizing about the relationship between QPPs in attention networks and the DMN has been the focus of this paper, building on previous investigations (Thompson et al., 2013; Abbas et al., 2019b). However, an intriguing aspect worth exploring is the relationship between the attention networks themselves. Although Petersen & Posner (2012) identified the regions of the FPCN as part of the TPN, our results suggest that the role this network plays in task performance may depend on an individual's current attentional state. During engaged attentional states, such as being in-the-zone, FPCN does indeed synchronize with DAN (*r* = 0.59), resulting in the canonical TPN identified by Petersen & Posner (2012). However, during out-of-the-zone periods, FPCN synchronizes instead with DMN and may be less appropriately characterized as "task positive." We also observed that the

FPCN and DAN exhibited an anticorrelation ($r = -0.95$) when subjects were out-of-the-zone. The two distributions of FPCN correlation with DAN within individual QPPs of the zone states also were significantly different $t(56) = 8.38$, $p < .001$, 95% CI [0.83, 1.35], in-the-zone (M = 0.43, SD = 0.51), out-of-the-zone (M = −0.66, SD = 0.48).

Research suggests a possible mechanistic explanation for FPCN that may clarify this change in activation pattern during different zone states. Specifically, FPCN may support sustained attention during in-the-zone state by synchronizing with an externally oriented network (DAN) or it may hamper sustained attention during out-of-the-zone states by synchronizing with an internally oriented network (DMN). Support for this comes from several sources. For example, Unsworth & Robison (2017) propose that FPCN activity suppresses DMN during externally demanding attention tasks. Further support for this idea comes from Spreng & colleagues (2013) who found evidence of FPCN mediating internal and external goals by flexibly coupling with DMN or DAN. Finally, the FPCN has been suggested to integrate information from DMN or DAN and as a result flexibly switching to either internal or external processing (Vincent et al., 2008; Dixon et al., 2018).

Interestingly, as opposed to the FPCN, the VAN was more anticorrelated with DMN in out-of-the-zone states rather than in-the-zone states (Fig. 4c). DMN tends to anticorrelate with both DAN and VAN at rest (Yousefi & Keilholz, 2021) and during periods of low arousal (Wang et al., 2016). Hence, it is not surprising that VAN and DMN pattern in out-of-the-zone state matches the QPP found in those state as the out-of-the-zone state seems more closely related to them than in-the-zone. What is peculiar is that VAN synchronizes more closely with DMN in in-the-zone than out-of-the-zone states.

Another observation is the synchronization of VAN and DAN, in the mean QPP of out-of-the-zone, the two networks exhibited highly positive correlation ($r = 0.92$) versus an anticorrelation ($r = -0.38$) when subjects were in-the-zone, $t(56) = -10.10$, $p < .001$, 95% CI [−1.26, −0.84], in-the-zone (M = −0.13, SD = 0.29), out-of-the-zone (M = 0.91, SD = 0.48). Previous studies have demonstrated the involvement of the DAN in goal-directed external attention, while the VAN has been associated with the alerting processes (Kim, 2014). Building on this knowledge, it is plausible that during the in-the-zone state, the FPCN collaborates with the DAN. Simultaneously, they may operate in opposition to VAN, potentially resulting in reduced alerting and distraction during sustained attention periods.

More task-based QPP research is warranted to elucidate the intricate relationships among these networks. Our study adds to the framework of sustained-attention proposed by Kucyi & colleagues (2017) (Fig. 6b) by using a novel time-varying functional connectivity method of the QPP analysis to understand the low-frequency fluctuation fluctuations correlated with sustained attention.

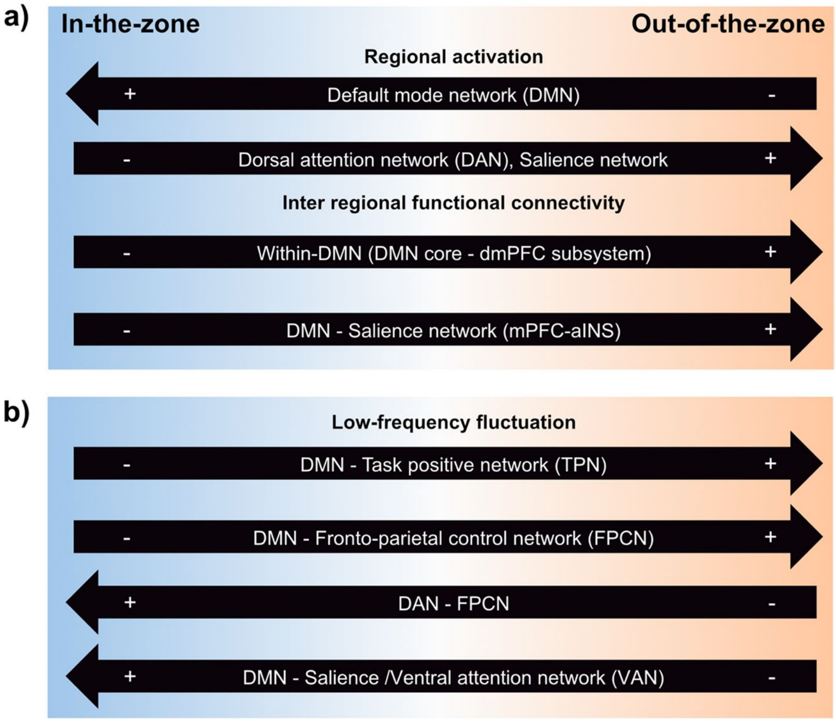

Fig. 6 Framework of sustained attention during zone state performance. (**a**) Regional activation and interregional functional connectivity (Kucyi et al., 2017). (**b**) Low-frequency fluctuation from our results

Discrepancy and limitations

In our study, we found that VAN (salience network) was positively correlated with DMN when participants were in-the-one and negatively correlated with DMN when they were out-of-the-zone. This appears to contradict the results from Kucyi & colleagues (2017) that reported the opposite relationship using static (cross-run) measures of connectivity. Research shows that QPP contributes significantly to the BOLD signal across runs (Abbas et al., 2019a, 2019b), so it is somewhat surprising that the current results do not align with Kucyi & colleagues. However, there are many differences between the studies that make direct comparison difficult. First, there are differences in the analyses. We removed global signal while Kucyi and colleagues did not report conducting global signal regression. Presence or absence of global signal is known to substantially alter functional connectivity (Murphy et al., 2009; Murphy & Fox, 2017; Yousefi et al., 2018). Furthermore, our signal was band-pass filtered between 0.01 Hz and 0.1 Hz as opposed the 0.01-Hz high pass that they applied to their data. Low-frequency fluctuations have been suggested to modulate long-distance neuronal synchronization, whereas high-frequency fluctuations are thought as localized regional network activity, hence the lack of representation of higher frequencies in our data could present divergent results (Von Stein & Sarnthein, 2000; Müller et al., 2011; Siegel et al., 2012). The different temporal frequencies may reflect different signaling along the same anatomical pathways (Helfrich & Knight, 2016). Finally, the QPP analysis is a different approach than the psychophysiological interaction (PPI) analysis that Kucyi et al. applied. Thus, it may be the specific patterns of DMN and VAN connectivity depend on inherent differences between the experiments, the analyses, or possibly the pattern is less reliable than previously proposed.

There are several possible limitations in this study. One is the potential for interference from the thought probes within each run (20s~ x 15 blocks). Signal from these probes also may affect the QPP. However, we used RT variability (Esterman et al., 2013) to determine which runs to include in each zone-state condition and found that these run-level behavioral differences were related to differences in run-level global state of brain network synchronization. While it is possible, we think it is unlikely that this finding is due to other—unmeasured changes—in the runs.

Another possible limitation has to do with when each zone-state condition occurred in the experiment. The in-the-zone runs tended to occur early in the session (median = 1, SD = 1.4), whereas the out-of-the-zone runs tended to occur later (median = 4, SD = 1.1), and the distributions are significantly different, $t(28) = -5.09, p < .05$. This is not surprising given the relationship between time on task, arousal, and attention (Pattyn et al., 2008; Langner & Eickhoff, 2013; Thomson et al., 2015). However, it is possible that some ancillary factors related to change in performance and dynamic connectivity change over time and that these factors contribute to the relationships discovered here.

Conclusions

This study is the first to employ low-frequency fluctuations with a network-based approach to understand the neural mechanisms of sustained-attention intra-individually. We found that the FPCN is important in integrating with DAN and disassociating with DMN for in-the-zone performance. Second, VAN works coherently with DMN during in-the-zone states in contrast with out-of-the-zone states. These results begin to identify the complex role these networks play in mediating attention across short time scales. More work is necessary to clarify the mechanisms for how these dynamic changes in activity and connectivity relate to the static changes previously described in the literature (e.g., investigating how preprocessing and processing strategies can affect the results) to mediate fluctuations in sustained attention.

Open practices statement Parts of the analyses were preregistered at https://osf.io/tcvgd. Data and materials for the experiment are available at https://osf.io/45ayg/?view_only=7238b505ee664b1f9d930e72a41080f9. Scripts for the QPP algorithm are openly available at https://github.com/GT-EmoryMINDlab/QPPLab. The rest of the preregistered analyses are beyond the scope of this paper and have yet to be completed.

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