

**TIME-VARYING FUNCTIONAL CONNECTIVITY PREDICTS  
FLUCTUATIONS IN SUSTAINED ATTENTION IN A SERIAL  
TAPPING TASK**

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The Academic Faculty

by

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In Partial Fulfillment  
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FLUCTUATIONS IN SUSTAINED ATTENTION IN A SERIAL  
TAPPING TASK**

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## **LIST OF SYMBOLS AND ABBREVIATIONS**

|      |                                 |
|------|---------------------------------|
| DMN  | Default mode network            |
| TPN  | Task positive network           |
| FPCN | Fronto-parietal control network |
| DAN  | Dorsal attention network        |
| VAN  | Ventral attention network       |
| SN   | Salience network                |
| QPP  | Quasi-periodic pattern          |

## SUMMARY

There is ambiguity in the literature about how large-scale brain networks contribute to focused attention. Part of the problem comes from the methods of analyses that treat the correlates of attention as a static and discrete measure when in actuality, attention fluctuates from moment to moment. This continuous change in attention is consistent with the dynamic changes in functional connectivity between brain regions involved in the internal and external allocation of attention (Liu & Dyun, 2013). Namely, the default mode network (DMN) and the task positive network (TPN)(Fox et al., 2005). In this study, I investigated how brain network activity varied across different levels of attentional focus (e.g., “zones”). Participants performed a finger-tapping task and, guided by previous research (Esterman et al., 2013), in-the-zone was marked by low reaction time variability and out-of-the-zone as the inverse. Employing a novel method of time-varying functional connectivity, called the quasi-periodic pattern analysis (i.e., reliably observed spontaneous low-frequency fluctuations), I found that the activity between DMN and TPN was more anti-correlated during in-the-zone states versus out-of-the-zone states. Further investigation showed that it is the fronto-parietal control network (FPCN) of the TPN that drives the differentiation. During in-the-zone periods, FPCN synchronized with the dorsal attention network, while during out-of-the-zone periods, FPCN synchronized with DMN. In contrast, the ventral attention network synchronized more closely with DMN during in-the-zone periods compared to out-of-the-zone periods. These findings suggest that time-varying functional connectivity in the low-frequency can tell us how different networks of the brain work together during periods of sustained attention.

## CHAPTER 1. 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, like understanding a lecture, to highly engaging ones like playing basketball. Some think of attention as a light— it's 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 within an individual as well as across more lengthy time periods (Macworth, 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 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) (c.f., Sarter et al., 2001).

### 1.1 Brain Networks of Sustained Attention

Cognitive neuroscientists have worked to understand the neural mechanisms related to sustained attention (e.g., Mesulam, 1990; Dockett 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 (c.f., Bressler and 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 fronto-parietal control (FPCN) networks (Fortenbaugh et al., 2017; Esterman & Rothlein, 2019; Zuberer et al., 2021) (Figure 1).

The DAN is hypothesized to mediate the 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 mediates executive control (Corbetta & Shulman, 2002; Vincent et al., 2008) and consists of the posterior dorsolateral prefrontal cortex (pDLPFC), the rostralateral 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 plays a role in monitoring for salient inputs. It is sometimes referred to as the salience or ventral salience network (Menon & Uddin, 2010). The main cortical brain regions in the VAN are composed of the anterior insula (AI) and dorsal anterior cingulate cortex (dACC). The model proposed by Bressler and 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 internal or externally directed goals (Vossel et al., 2014; Beaty et al., 2015). Together, the DAN, FPCN and VAN are known as the attention networks of the brain.

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), 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).



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

## 1.2 Ambiguity in the Literature

There is some disagreement in the literature on exactly what role these regions play in cognition. Some studies suggest that higher activity in the DAN can lead to more efficient performance (Padilla et al., 2006; Boly et al., 2007; O’Connell et al., 2009), cognitive flexibility (Leber et al., 2008), reduced distractibility (Leber 2010), and faster responding (Weissman et al., 2006). In contrast, Sadaghiani and colleagues (2009) found that an excessive increase in activity in DAN can be detrimental and lead to poorer target detection. Additionally, while higher DMN activity is said to contribute to mind wandering (Christoff et al., 2009), less efficient performance (Boly et al., 2007; Li et al., 2007; Eichele et al., 2008), and slower responding (Weissman et al., 2006), other research suggests that

moderately high activity in DMN can lead to better target detection (Sadaghiani et al., 2009), effortless performance (Mason et al., 2007), and faster responding (Gilbert et al., 2006; Hahn et al., 2007).

### *1.2.1 Reaction Time Variability as a Behavioral Correlate of Sustained Attention*

There may be multiple reasons for the ambiguity in the literature. A difficulty in studying sustained attention is finding a behavioral correlate of fluctuations of attention at timescales of a second or less. Classical vigilance tasks involve recognizing that a stimulus changes intermittently. This ability may fluctuate over minutes to hours (Macworth, 1948; Dorrian et al., 2004), but given the low rate of required overt responses, such tasks cannot differentiate fluctuations that takes place on faster timescales. More continuous tasks have been successfully used to measure attention at these timescales. For example, Conner's CPT-II (Conners, 1994), gradCPT, a gradual change detection task (Rosenberg et al., 2013; Esterman et al., 2013), sustained attention to response task (SART) (Robertson et al., 1997), finger tapping task, paced and self-paced (Seli et al., 2013; Kucyi et al., 2017), and breath counting test (Levinson et al., 2014) all have a high temporal sensitivity.

Additionally, while behavioral measures like error rates have been proposed to be good objective correlates to attention (Manly et al., 2000), Esterman and colleagues (2013) suggest 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) have also shown that deviations in performance variability correlate with mind wandering. In a recent experiment triangulating subjective experience with objective measures, Godwin and 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, intra-individual 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 an indicator of the level of sustained attention to a task.

Esterman and 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, that culminates in the perception of being in control. Esterman and colleagues speculate that *in-the-zone* captures the phenomenon *flow* (cf. Csikszentmihalyi, 1990). 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 under-engagement, capturing phenomena like boredom and mind wandering, to over-engagement, such as hyper-attentiveness due to 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 and 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 might be a tendency to mind wander and in turn cause a lapse in attention. Conversely, when participants were out-of-the-zone there was deactivation of the 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 and colleagues by RT variability.

### *1.2.2 Time-varying Functional Connectivity to Capture Attention Fluctuations*

Early studies of sustained attention using fMRI computed correlation across the duration of the scan for regions of the brain which can last from minutes up to an hour. This assumption of stationarity is problematic given the fluctuating nature of our attention. Additionally, researchers have found spatiotemporal activity and connectivity changes across seconds within a scan (Chang & Glover, 2010; Majeed et al., 2011; Liu & Dyun, 2013). Studies suggest that the time-varying properties of functional connectivity between regions can possibly produce different results depending on the timescale that is being used to investigate the activity of the regions (Allen et al., 2012; Handwerker et al., 2012; Hutchison et al., 2012). As a result, we may have contradictory claims that DMN and DAN can both support and be detrimental to performance. Esterman and 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 and colleagues (2017) employed a time-varying measure of functional connectivity which 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 SN in their study).

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

### **1.3 Framework of Sustained Attention**

Kucyi and colleagues (2017) proposed a framework for sustained attention (shown in Figure 6a). During in-the-zone periods of sustained attention, they saw 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 and 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.

Unfortunately, their framework focused on only the relationship between DMN and VAN. To attain a more complete understanding, our study investigates the inter-regional relationship between the attention networks (DAN, FPCN and VAN) and how they relate with the DMN. To do so, we employ a novel method that captures the repeating low-

frequency fluctuations between the brain networks called the quasi-periodic pattern (QPP) analysis.

#### **1.4 Repeating Low-frequency Fluctuations in the Brain: The Quasi-periodic Pattern**

In 1995, Biswal and 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. 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 EEG (Leopold et al., 2003; Helfrich et al., 2018), LFP (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 (Varela 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 and colleagues supported this notion that the neural mechanism of sustained attention is rhythmic by showing attention-related theta-band ( $\sim 4$  Hz) oscillations of frontal and parietal cortical areas (regions of the FPCN) using intracranial EEG. Using fMRI, Majeed and 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 anti-correlation between the BOLD signal of the DMN and the TPN. Since then, the QPP has been found in humans during resting-state and task scans (Abbas et al. 2019a), in rats (Majeed et al., 2009; Majeed

et al., 2011; Thompson et al., 2014), mice (Belloy et al., 2018), and macaques (Abbas et al., 2016) while awake or anesthetized. Most notably, the QPP is observed in humans during resting state and task (Majeed et al., 2011; Thompson et al., 2013; Abbas et al., 2019a). Of particular relevance to our study, in 2013, Thompson and colleagues discovered that faster response times on a psychomotor vigilance task were significantly associated with higher anticorrelation of the DMN and the TPN. In a following study, they proposed that this anti-correlation pattern that they found is related to the QPP (Thompson et al., 2014).

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). This leads us to hypothesize that neural oscillations of in brain association networks, measured with methods like ones identifying the QPP, may capture fluctuations of attentional focus that occur on the order of seconds rather than minutes or longer (c.f., Raut et al., 2021). In the current study, we test this by investigating the relationship between the QPP and RT variability related to different zone states during the performance of a continuous tapping task. We hypothesize that the QPP will show greater segregation between DMN and TPN during low RT variability (viz., in-the-zone) when sustained attention is high versus times of high RT variability (viz., out-of-the-zone) when attention lapses. Furthermore, with the QPP we can investigate how the subnetworks of the TPN (FPCN and DAN) and VAN relate to the DMN. Recent work demonstrated that while FPCN is part of the TPN, it has been seen to correlate with the DMN and anticorrelate with the DAN during resting state scans (Yousefi & Keilholz, 2021)

## CHAPTER 2. METHOD

### 2.1 Participants

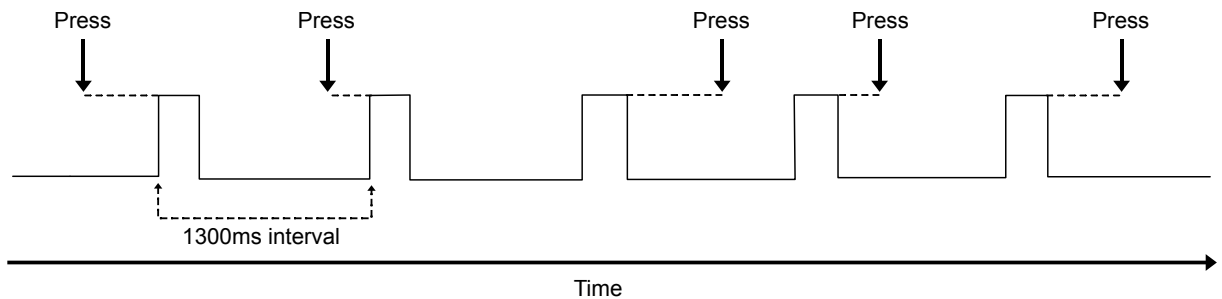
Using the dataset from Godwin and colleagues (2023), there were 31 participants with fMRI scans and behavioral data. Their age ranged from 18 to 23 ( $M = 20$ ,  $SD = 1.6$ ). They were right-handed, had normal or corrected-to-normal vision, and did not report prior neurological or psychiatric conditions. Two participants were excluded because their performance was below 90%, based on tap occurrence, leaving 29 participants (15 male, 13 female, and 1 gender-unidentified; average age:  $19.6 \pm 1.6$  years) in this analysis.

### 2.2 Task and Procedure

Participants performed a metronome response task (MRT) (c.f., 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 .77 Hz (one tone per 1300 ms) (Figure 2). A baseline fixation cross of 2-4s 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 16s, three blocks of 20s, two blocks of 24s, two blocks of 28s, one block of 32s, and one block of 36 s (run time = 10 mins and 33 seconds). 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 and colleagues (2023) for the results of the subjective analysis.



**Figure 2 - The serial tapping task.** Participants were instructed to tap along to a metronome tone as synchronously as possible. Each tone was 1300 ms apart.

### 2.3 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<sup>3</sup> voxels; flip angle = 9°; TE = 3.98 ms; TR = 2250 ms; and TI = 850 ms. Participants completed the experiment consisted of five runs, each for a total duration of approximately 10 min and 33s. Functional T2\*-weighted echo-planar 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<sup>3</sup> voxels; interleaved slice acquisition; gap = 0.5 mm; flip angle = 90°; TE = 30 ms; and TR = 2000 ms.

## 2.4 Behavioral Data Analysis

All tapping RTs were analyzed using Seli and colleague's method (2013) of calculating rhythmic response times (RRT) which is the difference in the time of a participant's pressing of the button response box time-locked to the metronome's tone onset time. RT variability for each run is calculated by taking the variance of each RRT within each run of the individual. Then a natural logarithm transformation was applied to adjust for the right-skewed distribution of RRT. 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 and colleagues (2013).

## 2.5 fMRI Data Preprocessing

Data preprocessing was performed using The Configurable Pipeline for the Analysis of Connectomes (C-PAC) (Craddock et al., 2013). This pipeline utilizes 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 done using the default settings of the C-PAC pipeline. Spatial smoothing was done 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, cerebral spinal fluid and white

matter signals were also regressed. 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 and colleagues (2018), which includes 400 defined regions of interest (ROI). The C-PAC pipeline is openly available at [www.nitrc.org](http://www.nitrc.org).

## **2.6 Quasi-Periodic Pattern Template Acquisition and Analysis**

A pattern-finding algorithm originally described by Majeed and colleagues (2011) and further refined by Yousefi and colleagues (2018) was applied separately to the concatenated brain sequences of all participant's in-the-zone and out-of-the-zone runs. The algorithm starts with selecting a time window of 20s starting segment. Then the algorithm uses a sliding window correlation method to search for other instances where the BOLD signal in the brain sequence correlate with the starting segments' peaks. As the search continues, additional segments are extracted and averaged, updating the segment. This process repeats itself until the search can no longer find variations to the latest updated segment. By averaging similar segments, the output is a template of a reliable repeating pattern of activity within the functional scan also known as the QPP template. The QPP template is dominantly characterized by an anti-correlation between the DMN and TPN. The code for QPP analysis is openly available at <https://github.com/GT-EmoryMINDlab>.

The QPP template is represented as a normalized time-course of activity in each ROI of the parcellated brain regions. By taking the average of the sum of the ROIs in each network, we calculated a mean BOLD signal during each timepoint (TR) for the DMN and TPN within each zone state. We also looked at the subnetworks of TPN (DAN and FPCN) and VAN's mean signal versus DMN within the QPP template. A positive correlation

indicates that the networks behaved similarly across time, while a negative correlation signifies a decoupling of the networks.

## CHAPTER 3. RESULTS

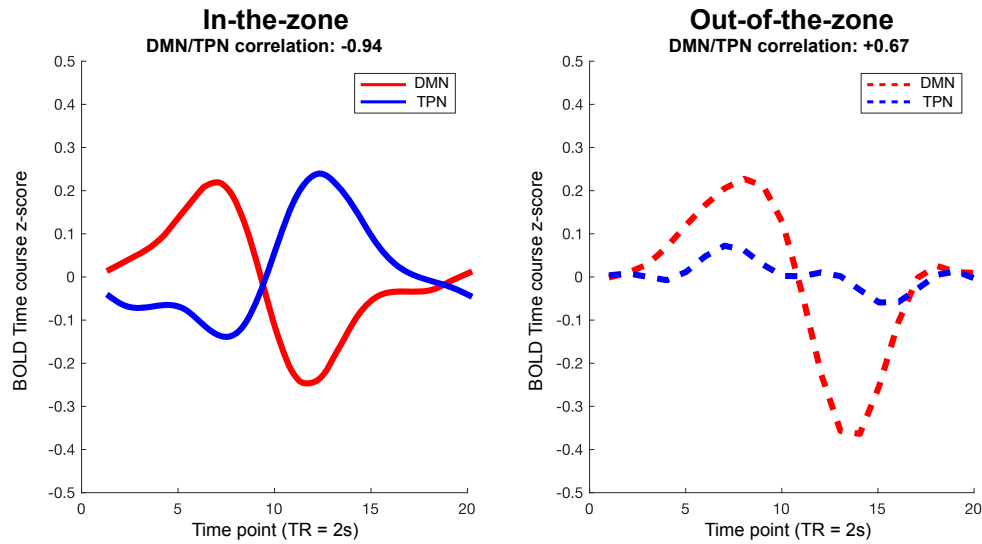
### 3.1 DMN and TPN Correlation Comparison Within Zone States

The resulting QPP template in the DMN and TPN in each zone state is shown in Figure 3. Pairwise correlations of the QPP template for DMN and TPN of in-the-zone (-0.94) and out-of-the zone (+0.67) were shown to be significantly different ( $p < .05$ ) using the following test (Olkin, 1967, pp 114-115):

$$\frac{\sqrt{n}[(r_{12}-r_{34})]}{\hat{\sigma}_{r_{12}-r_{34}}},$$

where

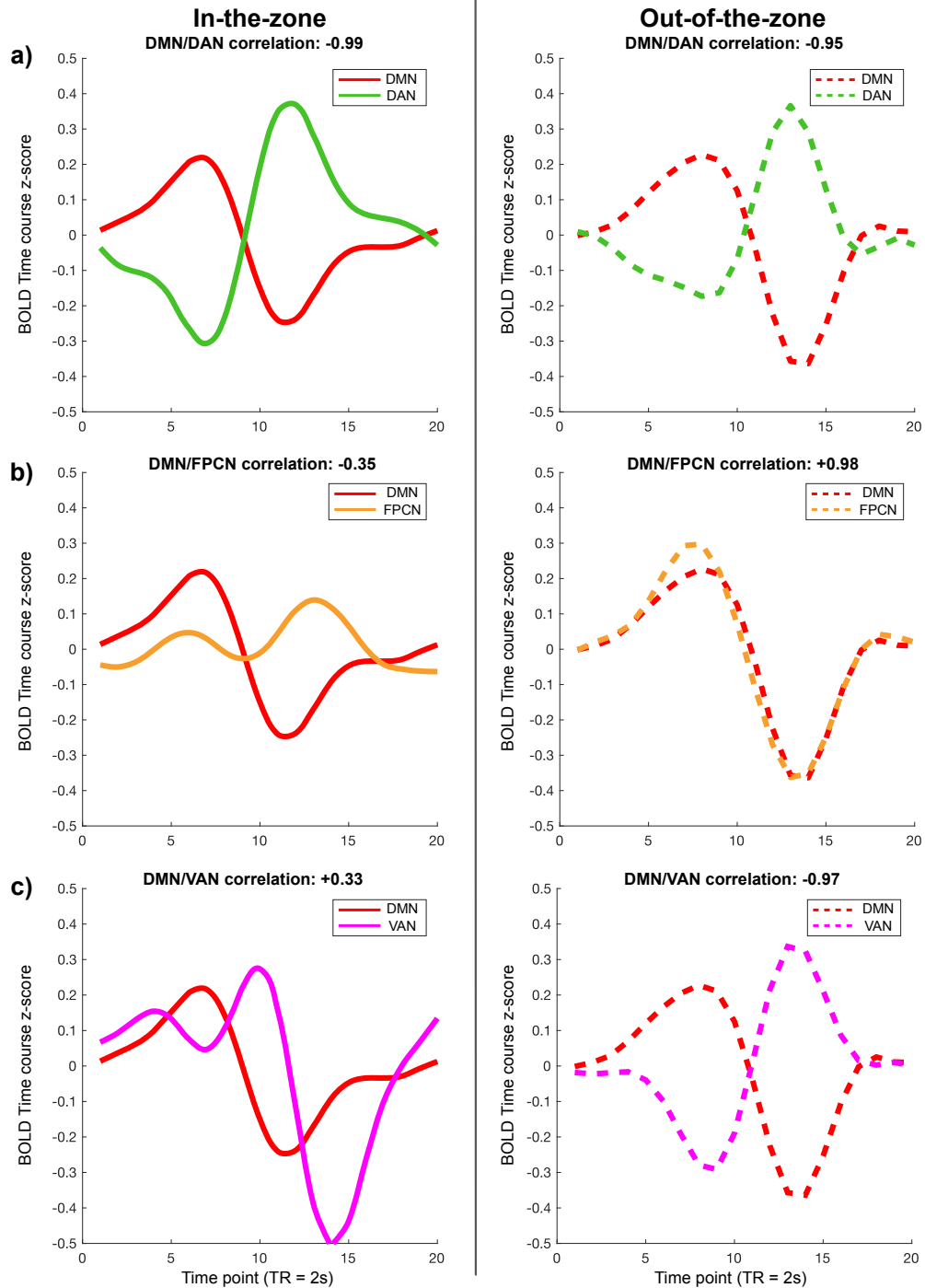
$$\begin{aligned} \hat{\sigma}_{r_{12}-r_{34}} = & (1 - r_{12}^2)^2 + (1 - r_{34}^2)^2 + r_{12}r_{34}[r_{13}^2 + r_{14}^2 + r_{23}^2 + r_{24}^2] + 2[r_{13}r_{24} + r_{14}r_{23}] \\ & - 2[r_{12}r_{13}r_{14} + r_{13}r_{23}r_{24} + r_{13}r_{23}r_{34} + r_{14}r_{24}r_{34}] \end{aligned}$$



**Figure 3 - The QPP template of DMN and TPN of in-the-zone has a negative correlation of -0.94 while out-of-the-zone has a positive correlation of +0.67 and they are statistically different ( $p < .05$ )**

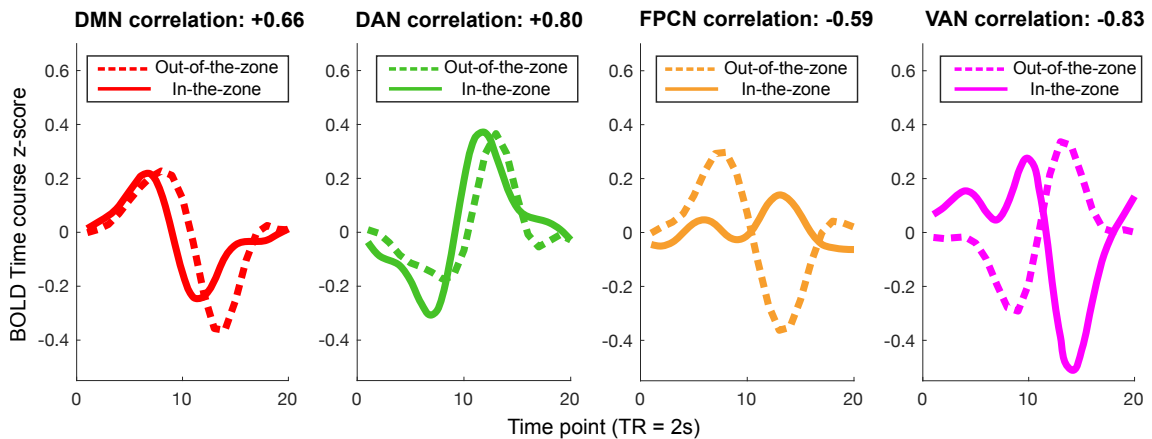
### 3.2 DMN's Relationship With DAN, FPCN, and VAN Within Zone States

To further interrogate the relationship of other networks hypothesized to play a role in sustained attention, we plotted all the subnetworks of TPN, and the VAN. As shown in Figures 4, DAN behaved similarly in both zone states (in-the-zone correlation with DMN = -0.99; out-of-the-zone correlation with DMN = -0.95). On the other hand, the FPCN correlated with DMN ( $r = +0.98$ ) while subjects were out-of-the-zone and decoupled from DMN while in-the-zone ( $r = -0.35$ ). VAN showed the opposite pattern to FPCN. It was positively correlated with DMN during in-the-zone runs ( $r = +0.33$ ) and negatively correlated with DMN during out-of-the-zone runs ( $r = -0.97$ ). Contrary to the significance test between DMN and TPN and the relative size of the differences here, none of these differences were significant using the test described previously.



**Figure 4 - Plots of each of the attention networks in relation to DMN** (a) DAN is not differentiated between the networks but is largely responsible for driving the anti-correlation of the QPP template (b) FPCN is less segregated from DMN in out-of-the-zone compared to in-the-zone (c) VAN is less segregated from DMN in in-the-zone compared to out-of-the-zone.

To further investigate how fluctuations in attention affected the QPP within networks, we compared each network across zone states (Figure 5). The DMN (+0.66) and DAN (+0.80) were similar in both conditions; whereas the FPCN from each zone state were significantly negatively correlated ( $r=-0.59$ ,  $p<.05$ ). Similarly, the VAN was significantly different across conditions ( $r=-0.83$ ,  $p<.05$ ).



**Figure 5 - The associations networks compared between conditions.** Both DMN and DAN reported a positive correlation denoting similar phase and magnitude. The FPCN in both zone states were negatively correlated which drove the difference between the DMN/TPN re relationship. The VAN reported the most difference between the conditions due to a flip in negative and positive phase.

## CHAPTER 4. 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 relate 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 (Figure 3). Additionally, we discovered that this change was primarily driven by attention-related changes in the FPCN. We also found that VAN activity differentiated attentional zone states (Figure 4 & 5).

### 4.1 DMN and TPN

As predicted, the QPP relationship between DMN and TPN during the in-the-zone condition (-0.94) was significantly more anticorrelated than out-of-the-zone's (+0.67) (Figure 5). That is, more successful sustained attention was associated with more segregation between these networks. This result complements prior research showing that faster response is associated with higher anti-correlation between DMN and TPN (Thompson et al., 2013). Moreover, Abbas and 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 has also been reported in many studies using static connectivity (Kelley et al., 2008; Hoekzema et al., 2013; Magnuson et al., 2015).

#### **4.2 DMN and The Subnetworks of TPN (FPCN and DAN)**

We found that the subnetworks within TPN were differentially related to zone state. Changes in FPCN connectivity across conditions drove 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 (Figure 4a & 4b). Further comparison of the FPCN from each zone state showed that they were significantly negatively correlated with each other (Figure 5). This reaffirms that what drives the significant difference between DMN and TPN correlation of the zone states stems from the FPCN. Previous research has shown that DAN and FPCN have different 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.

Although Petersen and Posner (2012) identified the FPCN as part of the TPN, our results suggest that it depends on the attentional state. During sustained attentional states like in-the-zone, FPCN does indeed synchronize with DAN, resulting in the canonical TPN identified by Petersen and Posner (2012). On the other hand, during out-of-the-zone periods, FPCN synchronizes instead with DMN and is less appropriately characterized as “task positive”.

Research suggests a possible mechanistic explanation of the role of FPCN that could explain this change in activation pattern during different zone states. Unsworth and Robison (2017) propose that FPCN activity suppresses DMN during externally demanding

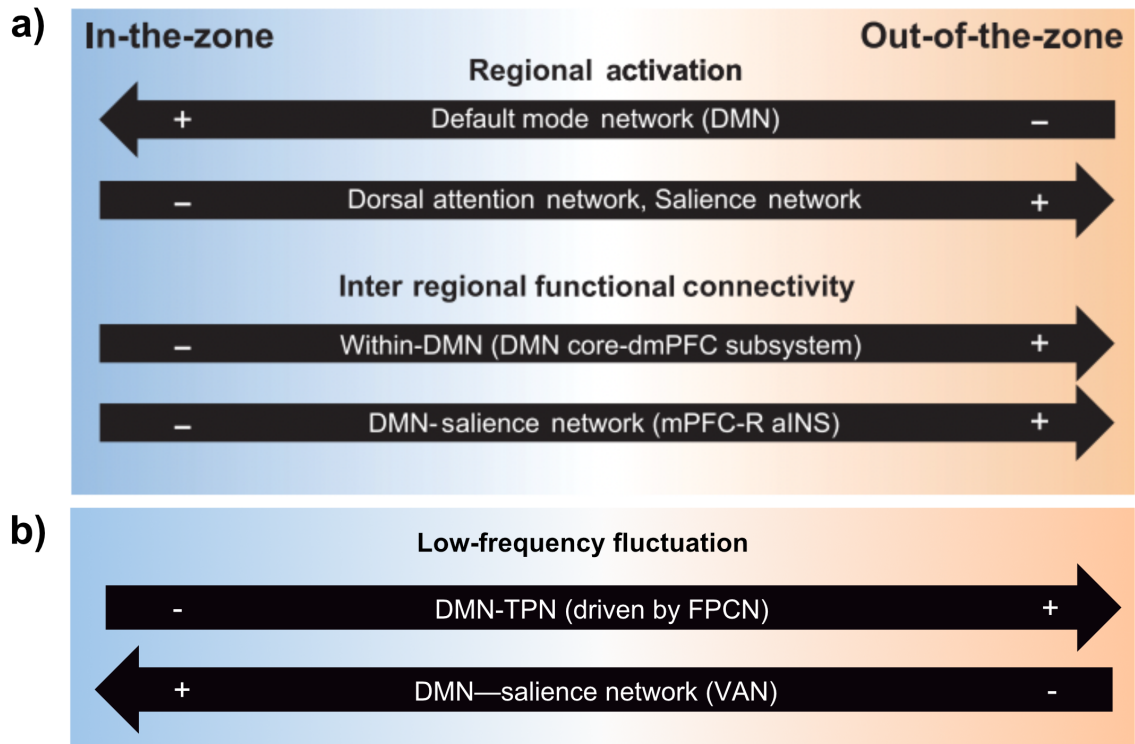
attention tasks. Further support for this idea comes from Spreng and colleagues (2013) who found evidence of FPCN mediating internal and external goals by flexibly coupling with DMN or DAN. These ideas are consistent with our data, FPCN may support sustained attention during in-the-zone state by synchronizing 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).

### **4.3 DMN and VAN**

Interestingly, as opposed to the FPCN, the VAN was more anti-correlated with DMN in out-of-the-zone states rather than in-the-zone states (Figure 4c). Recent interrogation of the QPP in resting state finds that DMN tends to anti-correlate with both DAN and VAN (Yousefi & Keilholz, 2021). Hence, it is not surprising that VAN and DMN pattern in out-of-the-zone state matches the QPP found in resting state scans as out-of-the-zone is more closely related to resting state than in-the-zone is. What is peculiar is that VAN synchronizes more closely with DMN in in-the-zone than out-of-the-zone states. More task based QPP research is needed to understand why that might be the case.

### **4.4 Neural Mechanism Framework of Sustained Attention**

Our study adds to the framework of sustained-attention proposed by Kucyi and colleagues (2017) below (Figure 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.



**Figure 6 - Framework of sustained attention during zone state performance** (a) for regional activation and inter regional functional connectivity framework (Kucyi et al., 2017). (b) low frequency fluctuation framework from our results.

#### 4.5 Discrepancy and Limitations

In our study, we found that VAN (salience network) was positively correlated with DMN when participants were in-the-zone, and negatively correlated with DMN when they were out-of-the-zone. This contradicts the results from Kucyi and colleagues (2017) that reported the opposite relationship. Research shows that QPP contributes significantly to the BOLD signal (Abbas et al., 2019a; Abbas et al., 2019b), so it is surprising that these results don't align. There may be multiple reasons for this discrepancy. First, there are many 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 0.1Hz as opposed to the 0.01 Hz high pass that they applied to their data. Low-frequency fluctuations have been suggested to modulate long-distance neuronal synchronization while 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, we used a parcellation based method to identify mean signal across all ROIs in each network. In contrast, Kucyi and colleagues used a seed-based approach. We attempted to rule out this last difference by taking the defined ROIs from their study of right mPFC (xyz = 6, 66, 4) and right aI (xyz = 40, 8, 0) and matched them with the closest parcel in Schaefer's 400roi parcellation. We then computed group functional connectivity in just these parcels. The results were more consistent with our QPP results (and inconsistent with Kucyi et al., 2017) where functional connectivity between the two regions was more negative in out-of-the-zone (-0.16) than in-the-zone (-0.13), but the minor difference was not significant and fails to resolve the discrepancy. Thus, it may be the specific patterns of DMN and VAN(SN) connectivity depend on other differences between the experiments, or the pattern is less reliable than previously proposed.

## CHAPTER 5. CONCLUSION

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. Secondly, 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.

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