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Dynamic functional connectivity of the default mode network tracks daydreaming☆

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ABSTRACT

Humans spend much of their time engaged in stimulus-independent thoughts, colloquially known as "daydreaming" or "mind-wandering." A fundamental question concerns how awake, spontaneous brain activity represents the ongoing cognition of daydreaming versus unconscious processes characterized as "intrinsic." Since daydreaming involves brief cognitive events that spontaneously fluctuate, we tested the hypothesis that the dynamics of brain network functional connectivity (FC) are linked with daydreaming. We determined the general tendency to daydream in healthy adults based on a daydreaming frequency scale (DDF). Subjects then underwent both resting state functional magnetic resonance imaging (rs-fMRI) and fMRI during sensory stimulation with intermittent thought probes to determine the occurrences of mind-wandering events. Brain regions within the default mode network (DMN), purported to be involved in daydreaming, were assessed for 1) static FC across the entire fMRI scans, and 2) dynamic FC based on FC variability (FCV) across 30 s progressively sliding windows of 2 s increments within each scan. We found that during both resting and sensory stimulation states, individual differences in DDF were negatively correlated with static FC between the posterior cingulate cortex and a ventral DMN subsystem involved in future-oriented thought. Dynamic FC analysis revealed that DDF was positively correlated with FCV within the same DMN subsystem in the resting state but not during stimulation. However, dynamic but not static FC, in this subsystem, was positively correlated with an individual's degree of self-reported mind-wandering during sensory stimulation. These findings identify temporal aspects of spontaneous DMN activity that reflect conscious and unconscious processes.

Introduction

Humans spend nearly half their time engaged in cognitions that represent stimulus-independent thoughts, colloquially known as "daydreaming" or "mind-wandering" (Killingsworth and Gilbert, 2010). A set of brain regions that could reflect daydreaming is the default mode network (DMN), which has ongoing activity during task-free and stimulus-free states that is suppressed during externally-oriented tasks (Raichle and Snyder, 2007). Evidence from functional MRI (fMRI) coupled with thought probes suggests that the DMN is activated during mind-wandering (Christoff et al., 2009; Kucyi et al., 2013). One DMN subsystem anchored in the dorsomedial prefrontal cortex is thought to subserve self-referential thoughts about the present. Another subsystem anchored in the medial temporal lobe has been associated with memory-based construction of future scenarios. The posterior cingulate and anterior medial prefrontal cortices may function as a DMN "core" because they co-activate and are functionally connected with both subsystems (Andrews-Hanna et al., 2010b).

The study of brain activity in an awake, task-free ("resting") state, in which daydreaming is a predominant activity, has recently emerged as an approach to understanding functional networks (Buckner et al., 2013). Brain areas with correlated oscillations, typically based on time series over 5–10 minute resting state fMRI (rs-fMRI) scans, are said to have functional connectivity (FC). This approach has revealed that the spatial organization of networks during rs-fMRI is surprisingly similar to that during unconscious states (e.g. sleep, anesthesia) (Horovitz et al., 2008; Vincent et al., 2007). However, network FC strength may vary for different cognitive states (Shirer et al., 2012) and consciousness levels (Vanhaudenhuyse et al., 2010). Therefore, in the awake resting state, how FC patterns reflect ongoing daydreaming,

Abbreviations: amPFC, anterior medial prefrontal cortex; DDF, daydreaming frequency; DMN, default mode network; dmPFC, dorsomedial prefrontal cortex; FC, functional connectivity; FCV, functional connectivity variability; MTL, medial temporal lobe; PCC, posterior cingulate cortex; rs-fMRI, resting state functional magnetic resonance imaging.

☆ This work was performed at Toronto Western Research Institute, University Health Network.

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versus neurophysiological operations that are independent of consciousness, remains unknown.

Conventional FC analysis, which assumes static connectivity over several minutes, may not capture dynamic thoughts spontaneously jumping from topic to topic. Recent studies demonstrated that FC fluctuates across shorter time-windows (e.g. 30–60 s) during rs-fMRI, with regions that are correlated with one another during some periods being uncorrelated and/or anticorrelated during other periods (Allen et al., 2014; Chang and Glover, 2010; Handwerker et al., 2012). Such dynamic FC fluctuations occur in anesthetized animals (Hutchison et al., 2013b; Majeed et al., 2011) and therefore cannot be explained purely by mind-wandering. However, fluctuating FC of specific networks might reflect daydreaming.

Here we propose that dynamic FC based on FC variability (FCV) between the DMN core and subsystems, across time-windows on the order of seconds, reflects mind-wandering. We previously demonstrated that individual tendencies to mind-wander away from painful stimulation are unrelated to the tendency to daydream (Kucyi et al., 2013). We showed that spontaneous FCV between the periaqueductal gray and medial prefrontal cortex was significantly correlated with individual differences in the tendency to mind-wander away from pain, but did not investigate the brain dynamics of general tendencies to daydream or fluctuations in mind-wandering states within individuals. The current study builds on and differs from our previous work as follows: First, we linked DMN FC and FCV with inter-individual differences in general tendencies to daydream. Then, we used thought probes during fMRI with painful stimulation to link the same metrics with intra-individual fluctuations in degree of mind-wandering (Fig. 1). Our unique paradigm enabled us to dissociate the components of spontaneous brain dynamics that relate to the general tendency to daydream across individuals versus the fluctuating state of daydreaming within an individual. We hypothesized that static DMN FC reflects largely unconscious brain operations related to the general tendency to daydream regardless of cognitive state, whereas dynamic DMN FCV reflects mind-wandering events.

Materials and methods

Participants

Fifty-one right-handed healthy volunteers (26 females, 25 males; mean age ± SD = 25.02 ± 2.68) participated in the study, as reported in a separate analysis (Kucyi et al., 2013). All of these subjects were included in resting state analyses, whereas only fifty were included in task fMRI analyses because one subject did not complete the task fMRI. Exclusion criteria included any history of neurological, psychiatric, or chronic illness, regular pain in the last six months, and medication use (besides birth control). Informed written consent was obtained for procedures approved by the University Health Network REB.

Assessment of daydreaming

We used two approaches to assess daydreaming. First, subjects completed the daydreaming frequency scale (DDF) of the Imaginal Processes Inventory (Singer and Antrobus, 1972) prior to MRI scanning on a different day. This provided a single overall measure for each subject of their propensity to daydream and allowed us to evaluate individual differences in brain connectivity related to individual propensity to daydream. DDF scores were normally distributed ($p = 0.78$, 1-sample Kolmogorov–Smirnov). Second, we used a thought probe method to determine when subjects were mind-wandering throughout an fMRI scan that included sensory stimulation (see below). This allowed us to evaluate connectivity dynamics related to intra-individual fluctuations in their state of mind-wandering (Fig. 1). To test whether the general tendency to daydream was dissociated from mind-wandering state during sensory stimulation, we calculated Pearson's correlation coefficient for DDF versus mean frequency of mind-wandering reports across the scans involving thought probes (two-tailed).

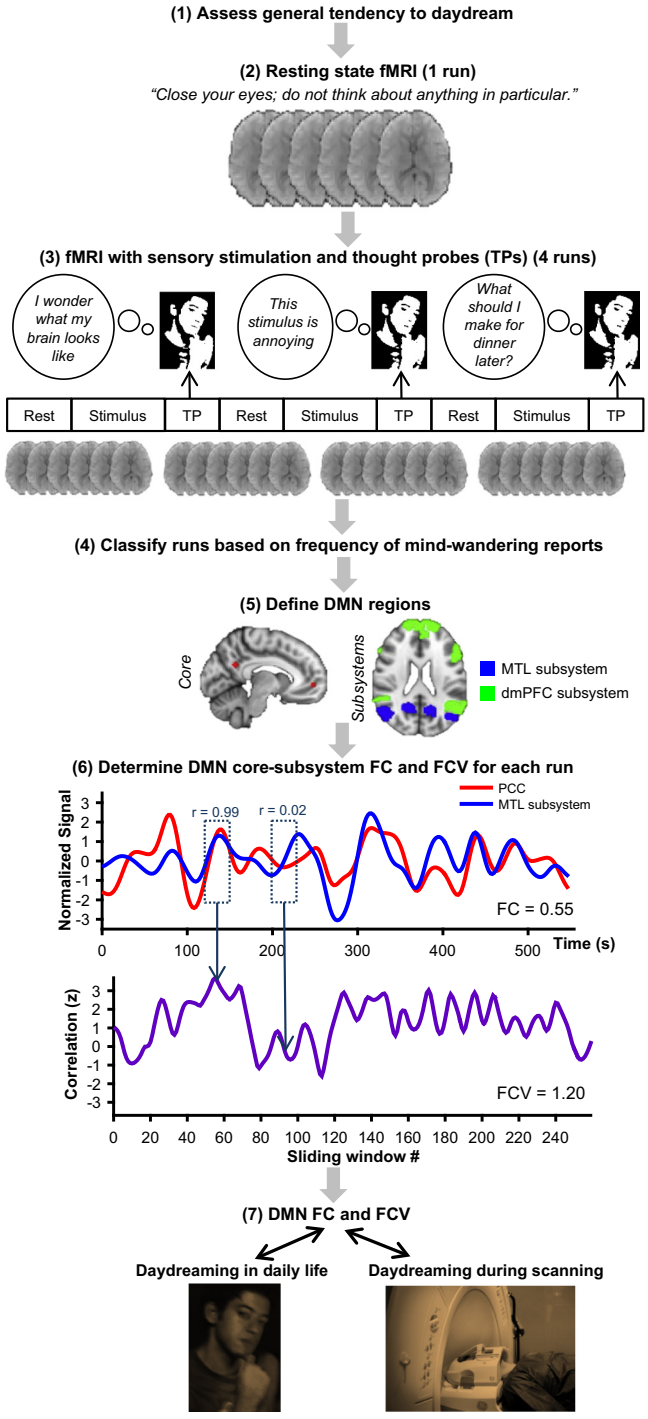

Fig. 1. Overview of the study's design and analyses. Subjects were assessed with a questionnaire for their general tendency to daydream (daydream frequency, DDF). They then underwent one run of resting state fMRI and four runs of fMRI coupled with sensory stimulation and thought probes. The runs with stimulation were classified based on frequency of mind-wandering reports. Regions of the default mode network (DMN) core and subsystems were defined. For each DMN core–subsystem pair, static functional connectivity (FC) and dynamic FC (based on FC variability (FCV)) was calculated within each run. A single-subject example is shown for fluctuations in the time series, and sliding window correlation series, for the posterior cingulate cortex (PCC) and medial temporal lobe (MTL) subsystem. The FC and FCV values were correlated with scores on the daydreaming frequency questionnaire and with intra-individual variability in run-to-run mind-wandering frequency during scanning.