On the nature of time-varying functional connectivity in resting fMRI

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Writing - review and editing: All authors.

Abstract

The brain is a complex dynamical system composed of many interacting sub-regions. Knowledge of how these interactions reconfigure over time is critical to a full understanding of the brain's functional architecture, the neural basis of flexible cognition and behavior, and how neural systems are disrupted in psychiatric and neurological illness. The idea that we might be able to study neural and cognitive dynamics through analysis of neuroimaging data has catalyzed substantial interest in methods which seek to estimate moment-to-moment fluctuations in functional connectivity (often referred to as "dynamic" or time-varying connectivity; TVC). At the same time, debates have emerged regarding the application of TVC analyses to resting fMRI data, and about the statistical validity, physiological origins, and cognitive relevance of resting TVC. These and other unresolved issues complicate the interpretation of resting TVC findings and limit the insights which can be gained from this otherwise promising research area. This article reviews the current resting TVC literature in light of these issues. We introduce core concepts, define key terms, summarize current controversies and open questions, and present a forward-looking perspective on how resting TVC analyses can be rigorously applied to investigate a wide range of questions in cognitive and systems neuroscience.

1. Time-varying connectivity: an introduction

Even when sitting quietly in a dark room, the brain is active—yielding a constant stream of thoughts and ideas, along with changes in awareness, arousal and vigilance. The brain constantly constructs and updates internal models of the world to anticipate and plan future adaptive behaviors (Parr, et al. 2018), and wakeful rest is no less cognitively rich and complex than task engagement. The notion that patterns of neuronal activity and inter-regional coupling may exhibit the statistical and dynamical fingerprints of these mental wanderings—even in the absence of an explicit task—accords with the most fundamental observations of our "stream of consciousness". While it is relatively straightforward to quantify changes in brain activity and connectivity that are time-locked to perceptual stimuli and externally cued tasks (Cohen 2017; Gonzalez-Castillo and Bandettini 2017), detecting and quantifying changes that arise "spontaneously"—from endogenous and unknown causes and at seemingly random times—is substantially more difficult. Fundamental questions remain about the nature of these changes and how best to detect them.

Functional connectivity (FC) analyses of resting fMRI (rfMRI) data allow researchers to non-invasively estimate patterns of inter-regional neural interactions. An integral component of modern neuroimaging research, FC is traditionally calculated over an entire scan or experimental condition ("static" connectivity), but recent years have seen rapidly growing interest in studying moment-to-moment fluctuations in FC (often referred to as "dynamic" or time-varying connectivity; TVC) (Calhoun, et al. 2014) (**Figure 1**). A burgeoning literature now spans studies using varied imaging modalities (e.g. fMRI (Hutchison, et al. 2013), EEG (Tagliazucchi, et al. 2012), and MEG (Baker, et al. 2014)) to investigate connectivity dynamics during a variety of task-free conditions including quiet rest (Allen, et al. 2014; Kucyi and Davis 2014; Sakoglu, et al. 2010), viewing of naturalistic stimuli (Simony, et al. 2016), sleep (Hutchison, et al. 2014) and anesthesia (Hutchison, et al. 2012). Inter-individual differences in resting TVC have been associated with a growing number of cognitive and behavioral traits including working memory, executive function and cognitive flexibility (Madhyastha, et al. 2015; Patanaik, et al. 2018; Rashid, et al. 2016). Preliminary evidence suggests that TVC may be a more sensitive measure of brain pathology than static FC (de Lacy, et al. 2017), and alterations of resting TVC have been observed in a wide range of psychiatric and neurological conditions including autism (de Lacy, et al. 2017), ADHD (de Lacy and Calhoun in press), depression, (Kaiser, et al. 2016), PTSD (Rashid, et al. 2014), schizophrenia (Diez-Cirarda, et al. 2018), Parkinson's (Diez-Cirarda, et al. 2018) and Alzheimer's disease (Jones, et al. 2012).

Like any emerging research program, resting TVC research has encountered its share of growing pains and challenges. Studying the brain at rest has a number of advantages— minimal demands on study participants, analytic flexibility afforded by the lack of an externally imposed task, the absence of potential performance confounds— and may potentially provide a richer characterization of brain activity (Ponce-Alvarez, et al. 2015) than task studies. However, while resting TVC research benefits from the advantages of rfMRI, it also suffers from its pitfalls: the lack of clear benchmarks, the absence of experimental control of behavioral or cognitive state, and the inability to objectively monitor behavioral task performance. Paralleling similar debates from the early days of rfMRI (see **Box 1**), there is active debate about the extent to which BOLD TVC is able to detect transient changes in neural signaling or cognition during rest. A number of important open questions contribute to this lack of consensus: To what extent are estimates of resting BOLD TVC driven by fluctuations in arousal and cognitive state versus non-neural physiological factors (e.g. head motion, cardiovascular and

respiratory effects) (Laumann, et al. 2016; Miller, et al. 2018)? What are the most appropriate ways to test observed estimates of TVC against "static" null hypotheses (Leonardi and Van De Ville 2015; Liegeois, et al. 2017; Miller, et al. 2018; Zalesky and Breakspear 2015)? Whereas detecting change-points or fluctuating dependence structure in neuroimaging data is in principle an achievable outcome of signal analysis—and indeed these are the goals of many TVC analysis methods— understanding the putative causes of these changes requires other techniques: online measures of cognition and bodily states, insights from pathological conditions, the inversion of generative models, and causal manipulations such as brain stimulation and administration of pharmacological agents. It is our goal to summarize the current literature surrounding these and related issues, and to provide suggestions for future work which may help adjudicate these debates.

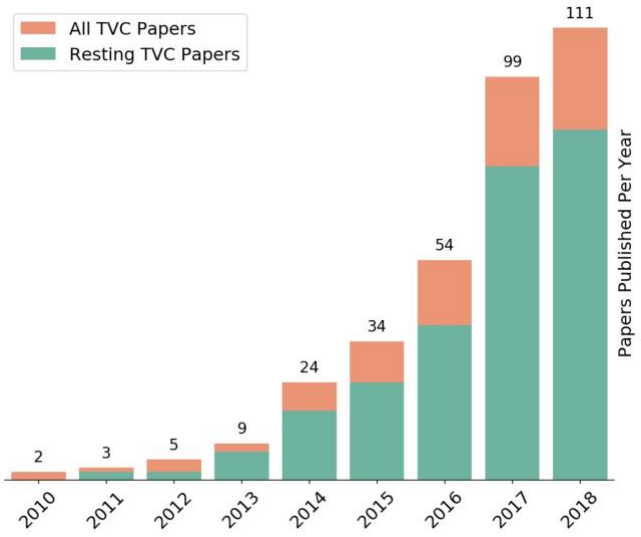

Figure 1: The field of TVC research has grown rapidly, as demonstrated by the increasing number of fMRI TVC papers published each year (as indexed by Pubmed as of early 2019). Due to inconsistencies in the way TVC analyses are described, these figures likely represent a conservative estimate of the size of the fMRI TVC literature, particularly for earlier years. For details on the search terms used to identify TVC papers, please see SI methods.

While there are indeed real points of fundamental disagreement among researchers about various aspects of BOLD TVC, debates in the literature have at times been needlessly muddied by inconsistent or imprecise definitions and operationalizations. For example, the term "meta-state" has been variously used to describe (i) a small number of replicable patterns of connectivity which recur across or within individuals (analogous to brain states) (Shine, et al. 2016b), (ii) subsets of brain states that share certain temporal characteristics (Vidaurre, et al. 2017b), or (iii) a specific location in a second-order state-space (Miller, et al. 2016). As has been previously suggested (Liegeois, et al. 2017; Miller, et al. 2018), we believe that progress on resolving these debates requires standardizing our terminology and identifying common frameworks. While intuitive notions of brain dynamics may seem straightforward, there is currently no consensus about operational definitions for many key concepts related to TVC. Establishing appropriate terminology for the phenomenon under study is particularly important. Although "dynamic connectivity" is frequently used in the literature, different uses and definitions of the term "dynamic" across disciplines can lead to troublesome ambiguity. As such, we have opted here to use the more broadly applicable phrase "time-varying connectivity", where connectivity refers to any of various notions of statistical dependence, most commonly (but not exclusively) correlation between time series. We define this and other key terms in the glossary presented in **Table 1**.

This paper is the result of a collaborative, open-invitation community effort to review the current resting TVC literature and to discuss key open questions and outstanding controversies regarding this exciting new domain of research. As a group of scientists with diverse perspectives on TVC, we have attempted to reconcile and synthesize our views on controversial issues, and to contextualize them in light of alternative opinions held by others in the community. While we offer some general suggestions for how researchers might best take advantage of the TVC research program, we avoid making specific technical or methodological recommendations except in cases where they are supported by the empirical literature.

We frame our discussion in terms of three broad questions: 1) Are rfMRI time series statistically consistent with functional connectivity that truly varies in time? 2) What is the biological basis of BOLD TVC (neural or otherwise)? 3) What (if any) is the cognitive and behavioral relevance of resting BOLD TVC? We begin with a survey of the current landscape of analytic and modeling approaches for studying BOLD TVC, and then proceed to address each of the three questions outlined above. First, we review methodological considerations and statistical challenges for studying TVC in rfMRI. Second, we review the literature on the physiological basis of BOLD TVC. Third, we provide an in-depth discussion of the cognitive and behavioral relevance of BOLD TVC, including evidence both for and against this proposition. Subsequent sections highlight experimental approaches which may help adjudicate questions about the cognitive relevance of TVC, and briefly review strategies for cleaning rfMRI data to mitigate the impact of potential confounds on TVC analyses. We conclude by suggesting ways that the TVC research community can continue to advance this exciting field and help facilitate consensus on current and future controversial issues.

2. Analytic Approaches

Approaches to studying functional connectivity in fMRI data can be considered along a spectrum of temporal resolution. On one end, static models assume that the dependence structure ("connectivity") between regions is constant over an arbitrarily long time window (i.e. static FC); on the other end are methods that can estimate time-resolved FC at each individual time point (e.g. instantaneous and sliding-window approaches). In between are models that aim to discover discrete, temporally contiguous brain states characterized by their inter-regional dependence structure (e.g. sliding windows + clustering). In these state-based models, the dependence structure changes only when moving *between* states.

Another important property of methods used to study TVC is the extent to which they consider the temporal ordering of the observed data points. Some approaches directly leverage the information in this ordering (e.g. time-frequency approaches (Chang and Glover 2010; Yaesoubi, et al. 2015)), while others ignore ordering completely and treat data points as exchangeable samples (Liu, et al. 2018; Yaesoubi, et al. 2018). Many common TVC analysis pipelines have stages that alternately leverage and neglect temporal ordering. For example, one might begin by estimating sliding-window correlations (calculated using time series with time points ordered as observed), apply k-means clustering to the resulting time-resolved connectivity matrices (k-means ignores the temporal ordering of the windows), and then evaluate state properties such as dwell times and transition probabilities (which again considers the temporal order of time points) (Allen, et al. 2014).

Beyond differences in temporal resolution and sensitivity to time point ordering, methods for studying TVC can be considered as taking one of two broad conceptual approaches to the challenge of studying brain dynamics. The first approach includes methods which attempt to estimate changes in connectivity (and/or identify connectivity states) directly from the observed BOLD data (e.g. sliding windows (Sakoglu, et al. 2010), clustering (Calhoun and Adali 2016), and HMMs (Vidaurre, et al. 2017b)). The second approach includes methods which explicitly model the neural processes underlying changes in the observed BOLD data (e.g. simulations of the brain as a dynamical system (Breakspear 2017; Park, et al. 2017)). These approaches are complimentary, and we expect future work on BOLD TVC to increasingly make use of these methods in combination. Below, we provide illustrative examples of each of the two approaches, but emphasize that these are not meant as a comprehensive review of all extant TVC methods. Rather, they are intended to provide a general idea of the breadth of available methodological approaches. **Figure *2*** illustrates common workflows for TVC analyses, while **Table 2** provides a selection of key papers on BOLD TVC and includes a number of recent reviews of TVC methods.

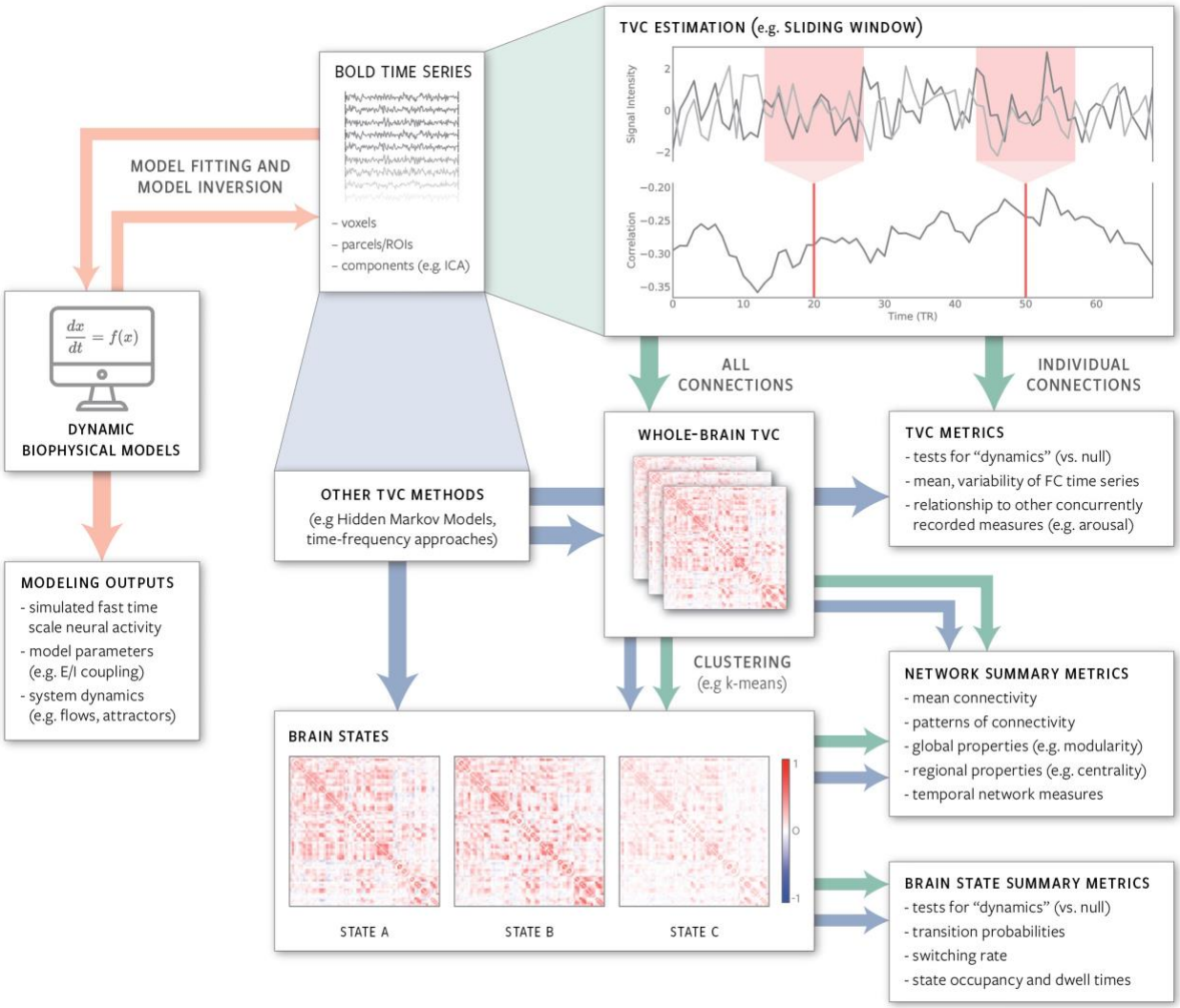

Figure 2: Schematic illustration of common analysis and modeling approaches for studying TVC in fMRI data. Green arrows indicate a typical workflow based on sliding-window correlation, which is currently the most common data-driven approach for estimating TVC. Blue arrows represent the diversity of alternative data-driven approaches. Some alternative approaches (e.g. HMMs) estimate brain states directly from BOLD time series, while others (e.g. phase synchrony, a time-frequency method) are more similar to the sliding-window approach. Regardless of how FC time series or brain states are estimated, it is possible to calculate a wide range of measures describing their properties. Whether TVC estimates are considered to constitute bona fide "dynamics" depends on the specific null model against which they are tested. Orange arrows represent a computational modeling workflow that fits a dynamic biophysical model to empirical BOLD time series in order to estimate model parameters and simulate underlying fast time-scale neural activity.

2.1 Example 1: Data-driven models of TVC

One family of approaches for investigating time-varying connectivity focuses directly on the observed BOLD signal without explicitly modeling the underlying neural activity. These techniques typically approach the observed fMRI data as multivariate time series and seek to identify the time-resolved dependence structure between them. The most widely used approach in this class estimates pairwise correlations within a sliding window, resulting in time-resolved correlation matrices (one per window) (Hutchison, et al. 2013; Sakoglu, et al. 2010). There are many variations on this theme, including the type of window used (square (Allen, et al. 2014), tapered (Allen, et al. 2014), or exponentially decaying (Lindquist, et al. 2014)), the flexibility of the window (fixed (Allen, et al. 2014) or adaptive (Lindquist, et al. 2014; Yaesoubi, et al. 2015)), as well as the length of the window (Leonardi and Van De Ville 2015; Liegeois, et al. 2016; Sakoglu, et al. 2010; Vergara, et al. 2017; Zalesky and Breakspear 2015). Other (windowless) methods estimate connectivity without assuming locality of the neighboring timepoints (Yaesoubi, et al. 2018), or utilize time-frequency

methods to estimate instantaneous connectivity using phase synchrony (Chang and Glover 2010; Pedersen, et al. 2018; Yaesoubi, et al. 2015). Regardless of the particular method used, a common next step is to assess the potential time-varying properties of the resulting time-resolved FC estimates, and to and explore possible associations with other dynamic phenomena (e.g. behavioral performance (Kucyi, et al. 2016; Patanaik, et al. 2018) or cognitive state (Kucyi and Davis 2014)). TVC estimates can also be summarized through the use of descriptive statistics (e.g. variance (Chang and Glover 2010; Kucyi, et al. 2013)) or methods which attempt to identify connectivity "states". Methods for identifying states include sliding windows + clustering (Allen, et al. 2014; Sakoglu, et al. 2010), Hidden Markov Models (HMMs) (Vidaurre, et al. 2017a; Vidaurre, et al. 2017b), change-point modeling (Cribben, et al. 2012; Xu and Lindquist 2015), and windowless dynamic connectivity (Yaesoubi, et al. 2018). After identifying states, it is possible to estimate a variety of parameters such as mean dwell times, transition probabilities, and graph theoretic measures that describe the observed connectivity patterns and brain dynamics (e.g. network modularity (Zalesky, et al. 2014)). These parameters can then be probed for association with measures of inter- or intra-individual differences (e.g. (Beaty, et al. 2018; Marusak, et al. 2018; Vidaurre, et al. 2017b)). State-based approaches can differ in whether they assume smooth transitions between states (Allen, et al. 2014; Ou, et al. 2015) or instantaneous reconfigurations (Liu, et al. 2018; Yaesoubi, et al. 2018), their focus on a particular signal domain (e.g. frequency (Yaesoubi, et al. 2015), time (Allen, et al. 2014), or space (Ma, et al. 2014)), and whether the state definitions are "hard" or "soft" (i.e., whether each time point exhibits a single state (Allen, et al. 2014) or is composed of a mixture of multiple states (Leonardi, et al. 2014; Miller, et al. 2016)). Temporal network theory, a subfield of graph theory, can also be used to quantify how network properties change over time (Holme and Saramäki 2012; Thompson, et al. 2017; Yu, et al. 2015). In all cases, it is critical to benchmark these statistics (i.e., the TVC estimates or state-related parameters) against those derived from reference data which embody a null or alternative hypothesis (e.g. that connectivity is "static" and does not in fact vary over time) (Thompson, et al. 2018). We return to the issue of null models in Section 3.1.

2.2 Example 2: Modeling the underlying neuronal dynamics

In contrast to methods which seek to analyze the observed BOLD signal directly, a second family of approaches instead aims to model the underlying neural fluctuations and interactions which give rise to BOLD TVC. This approach posits that observed BOLD time series are generated by underlying nonlinear brain dynamics which are then corrupted by measurement noise. Under this view, activity in large-scale neural systems is inherently dynamic and exhibits complex phenomena such as partial synchronization, multi-stable attractor landscapes, and edge-of-chaos behavior indicative of criticality (Cocchi, et al. 2017; Zalesky, et al. 2014). These dynamics generate physiological time series with highly nonlinear structure and can be formally modeled by biophysically derived differential equations. By combining these equations with models of the observation process (e.g. neurovascular coupling), it is possible to simulate how these underlying dynamics would manifest in the BOLD signal (i.e. after the addition of measurement noise). There are a wide variety of multi-scale models of interconnected pools of neurons, including neural mass and neural field models (Bojak, et al. 2010; Breakspear 2017; Deco, et al. 2008). These have been shown to produce neurobiologically plausible behaviors such as generalized synchronization, metastability, and multistability (Breakspear 2017; Deco, et al. 2008; Golos, et al. 2015; Heitmann and Breakspear 2018). Exploratory computational work involves adjusting the model structure and tuning parameters in order to obtain, through simulation, synthetic BOLD data that exhibits similar dependence and dynamics to empirical observations (Kashyap and Keilholz). Model-based approaches need to make strong assumptions about the processes which generate observed BOLD data (Deco, et al. 2008). Under these assumptions, it is possible to estimate from observed BOLD data the parameters of these models, and thus the underlying neural dynamics (including time-varying aspects) (Deco, et al. 2019). This process is known as model inversion. Models can be evaluated using a variety of methods (e.g. information criteria) which consider how well they fit observed data while penalizing model complexity. Careful model construction facilitates the testing of specific hypotheses about underlying dynamics, as well as validation of findings from approaches that model the BOLD signal directly (Zalesky, et al. 2014).

2.3 A rich diversity of methods for studying TVC

There is no single "best" method for studying time-varying connectivity; the choice of models should be informed by the available data and the particular questions under investigation. Different analytic approaches provide different (complementary) perspectives on the data, and a full understanding of TVC phenomena will likely necessitate integrating knowledge gained through the application of a wide variety of models (see **Box 2**). Some approaches (e.g. Example 1) make minimal (or no) explicit assumptions about the underlying biology, while others (e.g. Example 2) seek to model the

biophysical parameters directly. Improved biological specificity is often accompanied by greater model complexity and more extensive explicit model assumptions. That said, methods which directly model the observed BOLD signal can also be highly statistically articulated (e.g. HMMs) and come with their own assumptions (e.g. that the data are best represented by a limited number of states) which are often just as strong as assumptions made by biophysical models.

Highly articulated "data-driven" models (e.g. autoregressive models (Rogers, et al. 2010) or HMMs (Vidaurre, et al. 2017a)) may explain the data very well without recourse to biological assumptions, but do not provide information about the underlying neuronal dynamics without additional parameterization. As we learn more about brain physiology and dynamics, additional biologically informed constraints can be added to restrict the space of possible model solutions and improve the ability of these methods to accurately describe the neural processes underlying noisy BOLD data. In contrast, dynamical (nonlinear) systems theory provides an adequately rich parameterization to enable explicit exploration of how networks of neurons—modeled as coupled oscillators or populations of spiking neurons—may give rise to the observed BOLD signal. Scientific investigation of TVC is enriched by the application of both approaches, as they have complementary strengths, and the results from one perspective can inform the application of the other. For example, data-driven models of the observed BOLD signal can yield new biological hypotheses, which, if confirmed, can then be integrated into richer empirically-grounded dynamical models.

3. Statistical challenges in studying BOLD TVC

Before diving into questions about the biological basis and cognitive relevance of resting BOLD TVC, we must first ask whether there is statistical evidence for this phenomenon: Does functional connectivity estimated from resting BOLD fMRI actually vary over time? In this section, we discuss the importance of testing TVC estimates against null models, review the role of sampling variability in TVC estimation, and review approaches for evaluating and validating TVC methods.

3.1 The importance of testing against null models

Any method designed to estimate TVC will inevitably return time-resolved estimates of connectivity that vary to some degree with time (Lindquist, et al. 2014). Researchers must therefore carefully evaluate whether the observed TVC estimates significantly deviate from those that might have been obtained from time series generated by a process that lacks a particular property of interest (i.e., the presence of TVC). Such processes can be represented by reference to a suitable surrogate "null" distribution, typically generated through simulation or non-parametric resampling (Breakspear, et al. 2004; Prichard and Theiler 1994). Multiple methods have been developed to simulate surrogate data, including methods that represent a null model based on a specific system (Hindriks, et al. 2016), biophysical models which simulate different classes of dynamics in the brain (Heitmann and Breakspear 2018), and techniques that are designed to test the properties of specific methods used to estimate TVC (Allen, et al. 2014; Shakil, et al. 2016).

When evaluating observed TVC in this way, it is important to carefully consider both the features of the process used to generate null data, as well as the test statistic used to evaluate whether observed TVC estimates deviate from that null. For example, although some work has focused on statistical stationarity as a feature of null models (Laumann, et al. 2016), subsequent work (Liegeois, et al. 2017; Miller, et al. 2018) has clarified that the space of stationary models includes many processes that exhibit TVC (e.g., HMMs with switching covariance structure). Thus, statistical stationarity is not tantamount to static connectivity. Conversely, evidence of non-stationarity does not always imply the presence of a "meaningful" change and/or trend in the data (Koutsoyiannis 2011; Lins 2012). Likewise, it is also important to keep in mind that TVC estimates which fail to differ significantly from a static null do not necessarily equate to "meaningless fluctuations". Rather, such fluctuations could be consistent with a more restricted space of stationary stochastic models which may still have scientifically interesting properties (i.e. have heavy spatial and temporal tails (Cocchi, et al. 2017; Miller, et al. 2018; Roberts, et al. 2015)). This highlights the importance of carefully considering whether a null model corresponds to the intended test, and we encourage the TVC research community to work together to establish a consensus on which time series properties and null models are most appropriate for testing various aspects of TVC.

3.2 The role of sampling variability

Sampling variability is a key consideration for statistical inference. BOLD FC is typically estimated as the bivariate correlation between two time series, and a peculiar property of correlations of time series (first discussed over 90 years

ago (Bartlett 1935)) is that one can obtain high correlation coefficients even in the absence of a real relationship. This phenomenon (resulting from autocorrelation) can largely be summarized as an issue of sampling variability, which refers to how much a statistic varies across realizations of the data. The lower the sampling variability, the more precise the subsequent inference (e.g., confidence intervals and hypothesis tests).

As an example, consider the sampling variability of the sliding-window approach. Because sliding windows (and other TVC methods) estimate a series of correlations, it can be useful to think of these values as 'repeated samples' of correlations across time. From this perspective, the key question being asked when evaluating TVC estimates is whether each sample was drawn from the same distribution (static connectivity) or from distinct distributions (TVC). If we choose a small window size, the correlation coefficient will be based on few data points; this gives rise to larger sampling variability. Thus, short window lengths may give rise to signals that show compelling "dynamic" changes in correlation across time, even if the connectivity is actually static (Hlinka and Hadrava 2015; Leonardi and Van De Ville 2015; Lindquist, et al. 2014). This problem becomes less pronounced as window length increases, but longer windows come at the cost of reduced sensitivity to transient changes in correlation. In addition, if overlapping windows are used, an autocorrelation (beyond that already present due to the smoothness of the BOLD signal) is induced in the estimated TVC values, which can make changes in connectivity appear artificially smooth (Lindquist, et al. 2014). Recent work (Sakoglu, et al. 2010; Vergara, et al. in press; Vergara, et al. 2017) suggests that the optimal window length to minimize these concerns may be shorter than the ~60 seconds which has been previously recommended (Leonardi and Van De Ville 2015; Zalesky and Breakspear 2015), and one can consider the choice of window size to be a tunable filter which can be optimized based on the question of interest (Lindquist, et al. 2014; Vergara, et al. in press).

3.3 Establishing the sensitivity and reliability of TVC methods

Prior to the use of any new method, it is crucial to systematically evaluate the accuracy and reliability of its performance. One key metric of algorithmic accuracy is sensitivity, which for TVC methods is the ability to accurately recover TVC from noisy data. As the "ground truth" of TVC in the brain is often unknowable (and perhaps even undefined), evaluations of sensitivity typically make use of simulated data containing a known TVC signal of interest. Various simulation tools are available to help researchers evaluate how TVC methods perform under a range of different data-generating conditions (Allen, et al. 2014; Erhardt, et al. 2011; Heitmann and Breakspear 2017; Thompson, et al. 2018).

It is also critical to demonstrate that estimates of BOLD TVC are reliable enough to serve as robust markers of ongoing cognition and/or individual differences. Recent work has shown that whole-brain patterns of TVC at rest are largely reproducible across individuals (Abrol, et al. 2017; Choe, et al. 2017; Vidaurre, et al. 2017a), even when considering data from multiple scan sites and heterogeneous populations (Abrol, et al. 2017). Complementary work has shown that individual differences in resting TVC dynamics show good test-retest reliability (Choe, et al. 2017; Liao, et al. 2017; Liu, et al. 2017; Vidaurre, et al. 2017a). These studies satisfy an important prerequisite for continued research into resting TVC, and future work should continue to refine our understanding of which factors influence the reliability of these measures (Lehmann, et al. 2017). Additional work is also necessary to assess which properties of TVC are stable over time within an individual (i.e. "trait" characteristics) and which are modulated by the particular experimental context or cognitive state.

4. The biological basis of BOLD TVC

4.1 Cross-modal comparisons of BOLD TVC and direct measures of neural activity

fMRI is unique in its ability to non-invasively measure and localize activity simultaneously across the entire brain at relatively high spatial resolution. This has made it the modality of choice for many researchers interested in understanding large-scale brain dynamics (especially in humans). However, the BOLD signal is a noisy, indirect measure of the underlying neural activity, and sluggish neurovascular coupling places a fundamental limit on the temporal resolution of TVC estimated from fMRI data. We do not believe that these limitations preclude the use of fMRI for the study of TVC, but they do strongly motivate the need to validate and extend findings from fMRI through comparison with other modalities.

Studies of the neurophysiological basis of regional BOLD activity and static BOLD FC can help to provide a framework for investigating the neural basis of BOLD TVC. Intracranial recordings have consistently revealed a positive correlation between the BOLD signal and electrophysiological high-frequency broadband power (~50-150 Hz, also sometimes referred to as "high gamma"; (Logothetis, et al. 2001; Miller, et al. 2009; Mukamel, et al. 2005; Nir, et al. 2007; Scholvinck, et al. 2010). Further, static FC calculated from electrophysiological activity reliably exhibits similar topology to intrinsic BOLD FC networks when the two modalities are compared within the same individuals (Foster, et al. 2015; Hacker, et al. 2017; He, et al. 2008; Kucyi, et al. 2018a). However, it is unlikely that high-frequency broadband power is the only electrophysiological correlate whose FC mirrors that of the BOLD signal. BOLD FC also shows correspondence with inter-areal correlations in the band-limited power of lower frequencies, which can be detected using both MEG (Baker, et al. 2014; Brookes, et al. 2011; Hipp, et al. 2012; Hipp and Siegel 2015; Houck, et al. 2017) and intracranial recordings (Foster, et al. 2015; Hacker, et al. 2017; Wang, et al. 2012). The exact nature of this correspondence may be dependent on the specific frequencies and brain networks in question (Hacker, et al. 2017; Hipp and Siegel 2015).

Recently, multimodal recording approaches have been adopted to directly investigate the neurophysiological basis of BOLD TVC (see (Thompson 2017) for a review). These studies suggest that BOLD TVC may reflect fluctuations of electrophysiological FC across multiple frequency bands. Simultaneous fMRI and intracranial recordings in rats found that BOLD TVC between left and right somatosensory areas tracked changes in FC calculated from band-limited electrophysiological power, and that these associations exist across several canonical frequency bands (Thompson, et al. 2013b). Preliminary support for these relationships in humans comes from TVC analyses of simultaneously recorded EEG-fMRI data, which have found associations between BOLD TVC and changes in power across multiple frequency bands (Allen, et al. 2018; Chang, et al. 2013; Tagliazucchi, et al. 2012). Unfortunately, due to the poor spatial resolution of EEG, these studies are unable to speak directly to the electrophysiological basis of spatially specific variations in coupled activity between brain regions. However, studies using MEG (which provides improved spatial localization relative to EEG for many cortical regions) have also observed brain networks with similar topology to those found in fMRI, as well as time-varying inter-regional correlations of band-limited power on the scale of seconds to tens of seconds (de Pasquale, et al. 2010; Vidaurre, et al. 2018). As MEG cannot be recorded simultaneously with fMRI, the spatial and temporal correspondence of these effects with BOLD TVC remains uncertain.

There is good reason to believe that the heterogeneity of electrophysiological frequency bands reported as being associated with BOLD TVC is not merely artifactual or due to experimental variability. Different bands of electrophysiological activity likely reflect distinct neurophysiological processes (Buzsaki and Draguhn 2004). Recent work with human intracranial recordings, including within prominent nodes of canonical networks (e.g. default, dorsal attention), has revealed that different frequency ranges (e.g. high-frequency broadband versus alpha) of resting state TVC within a network often temporally diverge from one another (Kucyi, et al. 2018a).

Studies have shown that fluctuations in local field potentials at low frequencies directly comparable to BOLD fluctuations (<1 Hz) also contribute substantially to average measures of functional connectivity (Hiltunen, et al. 2014; Pan, et al. 2013). These infra-slow fluctuations in neural activity have been linked to quasi-periodic spatiotemporal patterns of BOLD fluctuations that involve coordinated propagation of activity across the brain (Grooms, et al. 2017; Thompson, et al. 2014b). A recent study in rodents found a close correspondence between windowed TVC calculated from optically imaged hemodynamic signals and simultaneously recorded calcium transients, and that variation in transient neural co-activation patterns was associated with fluctuations in windowed hemodynamic FC (Matsui, et al. 2018). Moreover, the observed TVC was not well explained by statistical simulations which assume stationary FC. Complementary work in humans has also successfully modeled BOLD TVC as being driven by transient periods of coordinated high-amplitude co-activations (Karahanoğlu and Van De Ville 2015; Tagliazucchi, et al. 2016). However, these findings must be considered in light of recent work suggesting that neural activity and changes in cerebral blood volume may become decoupled at rest (Winder, et al. 2017), as well as emerging research indicating that quasi-periodic patterns of BOLD activity may have different neural correlates than windowed TVC (Thompson, et al. 2014a; Thompson, et al. 2015). Overall, it seems possible (even probable) that multiple, dissociable neurophysiological processes simultaneously contribute to BOLD TVC. Indeed, it has been suggested that there is an "inverse problem" for BOLD functional connectivity in that there could be different underlying contributors at different moments (Leopold and Maier 2012).

4.2 Neuromodulatory influences on BOLD TVC

The effect of neuromodulators on neural activity and connectivity is a critical but often overlooked aspect of brain function. Regional and global release of these molecules can lead to drastic changes in the dynamics and functional connectivity of neural circuits (Bargmann 2012; Bargmann and Marder 2013), and it has often been suggested that neuromodulatory systems may play a key role in triggering and shaping the reconfiguration of functional networks across diverse behavioral states (Guedj, et al. 2017a; Hermans, et al. 2011; Shine, et al. 2018a; Shine, et al. 2019). In line with these theories, alterations of the neuromodulatory neurotransmitters dopamine (Alavash, et al. 2018; Shafiei, et al. 2018), noradrenaline (Guedj, et al. 2017b; Hermans, et al. 2011; Shine, et al. 2018a; Shine, et al. 2018b; van den Brink, et al. 2016), acetylcholine (Klaassens, et al. 2017), and serotonin (Klaassens, et al. 2017) have all been associated with significant alterations in the architecture and dynamics of BOLD FC networks. These studies typically involve a placebo-controlled design in which prior to scanning, subjects either ingest a pharmacological agent (e.g. a neurotransmitter agonist, antagonist, or reuptake inhibitor) or are administered a diet depleted in particular essential amino acids (e.g. tyrosine and phenylalanine) such that the stockpiles of neurotransmitters reliant on these chemicals for synthesis become exhausted. Given that these manipulations target endogenous neuromodulatory systems, it is reasonable to suspect that intrinsic and task-related fluctuations in neuromodulatory signaling may be a core mechanism underlying TVC. However, as neurotransmitters tend to have complex relationships with both neural activity and the hemodynamic response (Bruinsma, et al. 2018), care must be taken to ensure that the effects observed in fMRI studies of pharmacological manipulation are indeed related to changes in underlying neural activity (e.g. (Shine, et al. 2018b)), and not simply an epiphenomenon associated with alterations in the vasculature.

4.3 The role of arousal and sleep state in driving TVC

Arousal is an important dimension of brain function to consider when analyzing large-scale neuronal activity (Chang, et al. 2016; Larson-Prior, et al. 2009), especially when seeking to relate ongoing neural fluctuations to cognition (Larson-Prior, et al. 2009; Patanaik, et al. 2018). It has been known for some time that rfMRI connectivity patterns change when subjects fall asleep (Duyn 2011; Horovitz, et al. 2008; Tagliazucchi and Laufs 2014), even for very short periods of time (just a few seconds, i.e., "microsleeps"). While resting FC networks can still be detected in fMRI during sleep (Horovitz, et al. 2008; Larson-Prior, et al. 2009), they exhibit diminished temporal autocorrelation (Tagliazucchi, et al. 2013), and estimates of TVC are affected by fluctuations in drowsiness (Laumann, et al. 2016). Similarly, simultaneous EEG-fMRI studies have shown that EEG patterns known to occur during sleep correspond to distinct aspects of BOLD TVC fluctuations (Allen, et al. 2018; Damaraju, et al. 2017; Tagliazucchi and Laufs 2014), and some studies suggest that fluctuations in arousal may explain a large proportion of variance in TVC (Chang, et al. 2013; Laumann, et al. 2016; Tagliazucchi and Laufs 2014). This may pose a particular problem when comparing groups or individuals with differing levels of drowsiness (e.g. Parkinson's disease (Knie, et al. 2011)), and motivates the need to include sleep assessments and measurements of arousal in studies of static FC and TVC.

However, despite concerns raised by the association between level of arousal and BOLD TVC, it is important to note that sleep and level of arousal (as well as other global neuronal processes) often relate to cognition in non-trivial ways (Harrison and Horne 2000; Walker 2009). Changes in level of arousal are not purely binary (sleep vs. wake), but rather exist along a continuum. Subtle changes in arousal (e.g., epochs of heightened awareness/focus *vs.* epochs of relatively high distractibility (Pfaff, et al. 2012; Sadaghiani and D'Esposito 2015)) provide important constraints on cognitive processing (e.g. the vigilance required to detect subtly overlapping stimuli in continuous performance tasks (Rosenberg, et al. 2013)), while sleep deprivation and drowsiness can have a major negative impact on behavioral performance (Gillberg, et al. 1994). Given this close relationship between cognition and arousal, and the fact that fluctuations in arousal are largely driven by the activity of ascending brainstem neuromodulatory systems, it is perhaps to be expected that if TVC relates to cognition then it should also correlate at least moderately with arousal. Taking this perspective questions whether cognition and arousal effects on TVC can ever be adequately disentangled in a way that does not "throw out the baby with the bath water". Further, disambiguating the neural and physiological correlates of arousal from their consequences (e.g., changes in head motion, heart rate and respiration) is not straightforward, and thus caution should be taken in treating them as artifactual.

Beyond wakeful states, information processing and homeostatic processes which occur during sleep play a critical role in memory consolidation (Genzel, et al. 2014; McKenzie and Eichenbaum 2011; Walker 2009), and have been implicated in a wide range of cognitive processes including creativity and emotion regulation (Walker 2009). As such,

while TVC observed during sleep likely has little or no *immediate* cognitive or behavioral relevance, it may very well reflect important information processing that can impact subsequent waking thought and action. Such a perspective is consistent with the notion that TVC likely reflects a variety of conscious and unconscious cognitive process, as well as intrinsic non-cognitive processes (Kucyi 2017). Determining which (if any) aspects of BOLD TVC are sensitive to these "off-line" cognitive processes—as well as whether they can be distinguished from purely physiological homeostatic processes—will be a key challenge for our field.

5. Cognitive and behavioral relevance of resting BOLD TVC

A key attraction of BOLD TVC is the potential that it may be used to study the neural basis of cognition, which is an inherently dynamic process. There is growing consensus that fMRI is sensitive to changes in connectivity that accompany switches between externally cued tasks, and there is considerable interest in extending this work to studies of cognition during the resting state. While the unconstrained nature of the resting paradigm presents important challenges, it also provides exciting opportunities. Here, we review the evidence both for and against the cognitive relevance of TVC, with an emphasis on cognition during rest.

5.1 Evidence that time-varying connectivity is related to ongoing cognition and behavior

5.1.1 BOLD TVC tracks cognitive task performance

There is robust evidence that static BOLD FC patterns flexibly reconfigure across a range of experimental scenarios (Cohen and D'Esposito 2016; Cole, et al. 2014; Cole, et al. 2013; Gratton, et al. 2018; Mattar, et al. 2015; Shirer, et al. 2011; Xie, et al. 2019a; Xie, et al. 2019b) (see (Shine and Poldrack 2017) for a recent review of this literature). The most well studied examples involve the modulation of connectivity during cued cognitive task performance. In typical experiments, subjects are presented with one or more externally cued cognitive tasks and estimates are made of static FC during task performance. These studies are complemented by a growing literature on task-related TVC, which suggests that TVC measures are sensitive to fluctuations in short-timescale brain dynamics both across and within a wide range of behavioral tasks (Calhoun, et al. 2008; Cohen 2017; Ekman, et al. 2012; Gonzalez-Castillo and Bandettini 2017; Gonzalez-Castillo, et al. 2015; Sadaghiani, et al. 2015; Sakoglu, et al. 2010; Shine, et al. 2016a; Tobia, et al. 2017; Vidaurre, et al. 2017a). Together, these studies provide compelling evidence that the functional macroscale architecture of the brain as measured with BOLD FC is sensitive to the dynamics of cognitive and behavioral states.

Prior knowledge of stimulus timing and the ability to tie observed TVC to objectively measured fluctuations in behavior make task-based studies a highly interpretable validation of the cognitive relevance of BOLD TVC. However, this approach is not without criticism. It is possible that the TVC patterns associated with these tasks are altered by the somewhat artificial temporal, serial, and repetitive nature of most behavioral paradigms used in cognitive neuroscience. This problem may potentially be mitigated by using tasks with greater ecological validity (e.g., naturalistic viewing or listening; see below). In addition, task-related changes in estimates of FC can be driven by relatively trivial changes in coordinated activity, such as those resulting from stimulus-induced co-activation (Duff, et al. 2018). Several approaches exist which attempt to address this concern, including regression of stimulus-related effects (a.k.a. "background connectivity" (Norman-Haignere, et al. 2012)) and psychophysiological interaction models (PPI (O'Reilly, et al. 2012)). However, if the task model is at all mis-specified (e.g. the use of an incorrect hemodynamic response function, failure to model all relevant aspects of the task) then apparent correlations could still be driven by common stimulus-evoked activity rather than by inter-regional neural interactions *per se* (Cole, et al. 2018).

5.1.2 Stimulus-related cognitive dynamics and "pseudo-rest" paradigms

Paradigms with minimal explicit task demands but known time-varying stimulus properties may be particularly useful for establishing the immediate cognitive relevance of TVC in the absence of explicitly cued task switches. A growing number of experiments using "naturalistic stimuli" (e.g. free viewing or listening to movies or audio recordings) provide evidence that time-varying properties of the BOLD signal track fluctuations in stimulus-related cognitive state (Hasson, et al. 2004; Hejnar, et al. 2007; Lerner, et al. 2011; Nguyen, et al. 2017; Regev, et al. 2018). This type of experiment allows researchers to study correlated activity *across individuals* to identify brain areas whose fluctuations are temporally locked to features of a continuous complex stimulus. Because coherent inter-subject fluctuations (beyond perhaps those due to

study induced fatigue) are unlikely to occur during otherwise unconstrained listening/viewing, it is reasonable to attribute coherent brain changes across participants to fluctuations in cognitive, sensory, or emotional state induced by the stimulus.

The naturalistic stimuli and inter-subject correlation paradigm can be extended beyond single brain regions to the case of inter-subject and inter-regional correlations. For example, a recent study examined default network connectivity as subjects listened to a narrative and found that moment-to-moment network fluctuations were synchronized across individuals and could be reliably tied to narrative elements of the story (Simony, et al. 2016). Such fluctuating but consistent patterns of activity also co-vary with coherent inter-subject physiological fluctuations (such as heart rate-variability) (Nguyen, et al. 2016). These data provide further evidence that TVC methods can reveal subtle fluctuations in cognitive state, and suggests that variation in ongoing cognitive processes during task-free conditions can modulate the temporal structure of FC.

5.1.3 BOLD TVC and "spontaneous" cognition during the resting state

The absence of task instruction or experimentally controlled sensory stimulation does not imply the absence of ongoing cognition. Identifying the physiological and neural markers of ongoing fluctuations in cognitive and emotional states remains one of the core goals of cognitive neuroscience, and the application of BOLD TVC methods to these questions has the potential to provide new mechanistic insights.

Though it is well established that cognitive states fluctuate over short timescales, it remains unclear to what extent these fluctuations contribute to TVC at rest. As highlighted in previous sections, a broad consensus has emerged that there exist robust, reliable differences in BOLD activity and connectivity states between different externally cued cognitive tasks. However, compared to task-based studies, the effect of "spontaneous" fluctuations in mental state on brain activity at rest may be relatively small, and there are concerns about whether BOLD TVC methods are sensitive enough to detect these changes (Kucyi, et al. 2018b) (see section 5.2.3 for further discussion of this concern). Attempts to study the content, quality, and dynamics of "spontaneous" cognition—which occur on unpredictable and uncontrolled timescales—pose a significant experimental challenge. "On-line" measurement methods such as thought probes and experience sampling can provide relatively frequent self-reports of mental state (Christoff, et al. 2009; Kucyi and Davis 2014; Kucyi, et al. 2016) but at the risk of inducing an "observer effect" that might potentially influence the cognitive processes under study (e.g. by introducing an implicit task demand of metacognitive monitoring). Retrospective reports (e.g. post-scan questionnaires (Diaz, et al. 2013; Gorgolewski, et al. 2014)) avoid this potential pitfall, but at the cost of significantly reduced temporal resolution.

Despite these challenges, many fundamental questions about the relationship between TVC and ongoing cognition necessitate the application of these methods, and there exists an emerging literature demonstrating their feasibility and utility (Kucyi, et al. 2018b). Numerous studies suggest that BOLD TVC is associated with a variety of "spontaneous" cognitive dynamics including memory reactivations (Tambini and Davachi 2013), variations in perceptual performance (Sadaghiani, et al. 2015; Thompson, et al. 2013a), changes in arousal indexed by pupil diameter (Shine, et al. 2016a), and self-reported stimulus-independent thoughts (Chou, et al. 2017; Kucyi and Davis 2014; Kucyi, et al. 2013; Marusak, et al. 2018; Mittner, et al. 2014). Although these studies did not all include 'pure rest' conditions, the types of cognitive processes they investigated are all likely to fluctuate during typical wakeful rest. The extent to which such processes are separable from one another remains an open question, but these methods can be complemented by simultaneous recording of physiological signals (e.g. eye tracking, cardiac and respiratory monitoring) to assess the extent to which observed changes in TVC are driven mainly by the content/quality of cognition versus concomitant physiological processes.

5.2 Reasons for skepticism regarding the cognitive relevance of resting BOLD TVC

While there is a rapidly growing literature on the cognitive relevance of resting BOLD TVC, there remain reasons for skepticism. Below, we review three lines of evidence that raise important questions about which cognitive and physiological factors drive observations of resting TVC, as well as the extent to which brain networks reconfigure in response to changes in cognition and behavior.

5.2.1 TVC during anesthesia

Some of the strongest evidence against the cognitive relevance of BOLD TVC comes from studies which have shown that TVC is present during unconsciousness due to general anesthesia (Barttfeld, et al. 2015; Hutchison, et al. 2012; Liang, et al. 2015), when one should expect no changes in cognitive state or level of arousal. Indeed, a number of studies which helped to establish a neural basis for BOLD TVC made use of simultaneous electrophysiological and fMRI recordings from anesthetized animals (e.g. (Thompson, et al. 2013b)). These results suggest that at least some fraction of BOLD TVC must be reflective of non-cognitive intrinsic or homeostatic processes. That said, studies have also found differences in the characteristics of TVC observed during wakefulness vs. anesthesia. For example, there appear to be a larger repertoire of TVC states observed when monkeys are awake than when sedated, including more anticorrelated connections and states that deviate from the underlying structural connectivity (Barttfeld, et al. 2015). Similarly, brain activity in rats undergoing progressive levels of anesthesia visits fewer distinct states and exhibits fewer transitions as anesthesia deepens (Hudetz, et al. 2015; Hutchison, et al. 2014; Ma, et al. 2017). While these studies demonstrate that some aspects of TVC in the awake condition are distinct from the anesthetized condition, other TVC properties were remarkably similar between the conditions. The sedated animals still displayed state switching patterns, and the duration spent in each state was comparable to the awake condition. A key challenge going forward will be to determine which TVC properties (if any) are specifically sensitive to fluctuations in cognitive state rather than the kind of intrinsic brain dynamics present during unconsciousness.

5.2.2 Confounding by head motion

Head motion during scanning is likely one of the most significant confounding factors influencing the estimation of BOLD functional connectivity (Power, et al. 2012; Van Dijk, et al. 2012), and numerous papers have demonstrated that even very small amounts of head motion can result in biased estimates of static FC (Power, et al. 2015; Satterthwaite, et al. 2012). Some recent work has suggested that head motion may lead to similarly biased estimates of TVC, and that current tools to reduce these effects may not be sufficiently effective (Laumann, et al. 2016). In contrast, other studies suggest that head motion may have only a small impact on TVC measures and their reliability (Abrol, et al. 2017). There is a pressing need for additional work in this area to help establish a more robust understanding of the extent to which different aspects of BOLD TVC are influenced by head motion, and to identify effective data cleaning strategies.

5.2.3 Stability of functional connectivity networks

Much of the interest in rfMRI FC over the past two decades has been due to its high reliability. Resting static FC can provide a robust estimate of an individual's functional network architecture which is stable across multiple scans and imaging sessions, even months or years apart (Guo, et al. 2012; Shehzad, et al. 2009; Wang, et al. 2011). This kind of reliability suggests that patterns of static FC may be relatively insensitive to fluctuations in cognitive state, and there is growing evidence to support this hypothesis. Studies have shown that static FC networks during task and rest are highly similar, correlating at up to r=0.9 (Calhoun, et al. 2008; Cole, et al. 2014; Geerligs, et al. 2015; Gratton, et al. 2018). Patterns of static FC are are also quite stable across different tasks, with similarity estimates ranging from r=0.5 to r=0.9 (Cole, et al. 2014; Finn, et al. 2017; Geerligs, et al. 2015; Gratton, et al. 2018; Krienen, et al. 2014). Taken together, these studies demonstrate that even the largest reconfigurations of static FC across cognitive states are relatively subtle, and that small changes to a largely stable underlying functional network architecture may be sufficient to produce a wide variety of cognitive and behavioral states. Still, given that variation in static FC network structure is small even between behaviorally distinct states (e.g. task vs. rest), some researchers have expressed skepticism about whether endogenously driven fluctuations in resting cognition will have any observable influence on BOLD FC. These concerns underscore the importance of developing and utilizing statistically robust TVC methods, as well as effective data-cleaning strategies; in their absence, researchers seeking to associate resting TVC with cognition will have great difficulty convincing skeptics that observations of resting TVC are due to cognitive processes rather than confounds such as head motion or sampling variability.

5.3 Future directions in studying the cognitive relevance of BOLD TVC

Given the lack of consensus as to the cognitive relevance of BOLD TVC, it is clear that more work is needed to adjudicate this controversy. While there are many different ways to approach this problem, here we focus on two approaches which we feel are of particular interest and utility.

5.3.1 Continuous task paradigms

Many studies of task-evoked changes in brain connectivity explicitly test for differences in connectivity between two or more cognitive states that are either imposed by the experimental paradigm or inferred from post-hoc analysis of behavioral performance. Often, these states are split across multiple scans. However, a growing number of studies make use of continuous task paradigms in which task demands change over the course of a single scan (Gonzalez-Castillo, et al. 2012; Xie, et al. 2017). Data from such experiments can provide a powerful opportunity to test the sensitivity of methods for estimating BOLD TVC and identifying brain states. Given an fMRI time series that spans multiple cognitive or behavioral states (as imposed by the experimenter or inferred from analysis of behavior), the validation question becomes whether our statistical methods are able to identify—directly from the fMRI data— fluctuations in BOLD FC or derived brain states which track the experimentally imposed (or behaviorally defined) conditions. Methods which show promise in reliably identifying TVC fluctuations and brain state transitions that align with known shifts in cognition and behavior will be best suited for studying BOLD TVC at rest, where states and transitions are not known a priori.

5.3.2 Causal manipulation of TVC via brain stimulation

Brain stimulation technology is evolving rapidly, and recent years have seen the development of methods such as transcranial electrical stimulation—tACS (Ali, et al. 2013; Helfrich, et al. 2014) and tDCS (Keeser, et al. 2011; Polania, et al. 2011; Polania, et al. 2012; Sehm, et al. 2012)—and rhythmic TMS (Hanslmayr, et al. 2014; Romei, et al. 2016; Thut, et al. 2011a; Thut, et al. 2011b) that may allow for the experimental modulation of inter-regional neural synchrony. While some controversy remains as to the efficacy and reliability of these methods (Lafon, et al. 2017; Voroslakos, et al. 2018), they suggest an exciting opportunity for researchers interested in TVC. It may soon be possible to induce particular patterns of TVC in human subjects while they sit quietly at rest or engage in an experimental task. Changes in cognitive state or behavioral performance that reliably track experimentally induced TVC would provide causal evidence for the cognitive and behavioral relevance of TVC phenomena. Complementary work using simultaneous brain stimulation and fMRI could help to further uncover the precise neural basis of BOLD TVC, for example by varying stimulation across frequency bands and measuring at which frequencies connectivity modulation has the greatest impact on estimates of BOLD TVC. In this vein, recent work using direct intracranial brain stimulation in neurosurgical patients (single pulse stimulation to measure cortico-cortical evoked potentials in target regions) has begun exploring the relationship between the organization of BOLD FC networks and stimulation-evoked responses (Keller, et al. 2011; Shine, et al. 2017), and we expect that these and similar methods will see increased use in the coming years.

6. Cleaning data for TVC analysis

Preprocessing plays a critical role in removing confounds (e.g. head motion, cardiac and respiratory signals) prior to analysis of fMRI data, and this is particularly true when working with data acquired during rest. While most standard rfMRI pre-processing steps (Caballero-Gaudes and Reynolds 2017) are applicable to TVC analyses, certain steps require that special care be taken. It has recently been observed that although nuisance correction occurs prior to TVC estimation, correlations with nuisance regressors can reemerge once TVC has been calculated (Nalci, et al. 2018). For sliding-window analyses, given a window of length ω, it has been recommended to remove frequency components below $1/\omega$ (Leonardi and Van De Ville 2015) (although recent work suggests shorter windows may provide improved accuracy when using TVC estimates to predict phenotypic characteristics (Vergara, et al. 2017; Zalesky and Breakspear 2015)). Finally, there is evidence that time series autocorrelation may influence TVC estimates (Lehmann, et al. 2017), and that removing the effects of autocorrelation through pre-whitening the data may decrease sampling variability (Liegeois, et al. 2017). Together, these findings suggest that TVC-specific nuisance cleaning pipelines may be needed to optimally remove the effect of movement and other signals of non-interest (Gargouri, et al. 2018; Lydon-Staley, et al. preprint; Vergara, et al. 2017; Vergara, et al. 2018).

In addition to preprocessing, when comparing TVC measures between groups it is important to undertake control analyses to ensure that observed differences in TVC are not driven by systematic artifacts (e.g. group differences in head motion). This can be done by directly comparing potential confounding factors between groups, or by testing for a correlation between potential confounds and TVC measures of interest. It is also possible to test for residual confounding after preprocessing and compare these residual estimates between groups (Ciric, et al. 2017; Parkes, et al. 2018).

6.1 Minimizing the influence of head motion

A number of recent studies have attempted to benchmark the effectiveness of different pipelines for mitigating the effects of head motion on estimates of BOLD FC (Ciric, et al. 2017; Parkes, et al. 2018). Consistent results suggest that pipelines which include ICA denoising and global signal regression (GSR) may be most effective. However, to our knowledge, only one study has so far attempted a systematic comparison of motion denoising pipelines specifically for TVC analyses (Lydon-Staley, et al. preprint). As is the case for static FC, motion contamination of TVC estimates was minimized most effectively by pipelines that included GSR, though it should be noted that in general the use of GSR is somewhat controversial (Murphy and Fox 2017). It is important that this new work be replicated and expanded upon to begin building a consensus on optimal data cleaning strategies for TVC analyses.

Volume censoring ("scrubbing" (Power, et al. 2012)) is another commonly used method to minimize the effects of head motion on FC estimates. By removing volumes with high levels of motion, the issue of motion contamination is essentially sidestepped. Censoring can be very effective in studies of static FC (e.g. (Power, et al. 2014)), and recent work suggests that it may be similarly powerful in the context of TVC (Laumann, et al. 2016). However, because censoring disrupts the temporal relationship between time points, it can interact in undesirable ways with subsequent TVC analyses which implicitly or explicitly consider these factors. For example, censoring prior to sliding-window analysis can result in windows which contain unequal numbers of time points (Hutchison, et al. 2013; Zalesky, et al. 2014), and time series with uneven spacing between time points due to censoring are incompatible with most time-frequency based approaches.

6.2 Accounting for arousal-related effects

As discussed in depth in Section 4.3, several studies have shown that changes in vigilance and arousal can impact measures of brain function. While the ability to detect changes in arousal can be considered a strength of TVC, it can also be considered a potential confound. Studies that wish to make inferences about the cognitive relevance of TVC (or compare TVC between groups) independent of arousal must therefore measure and account for the presence and influence of these fluctuations. Although it can be difficult to track subtle fluctuations in arousal, measurements of pupil diameter (Allen, et al. 2018; Schneider, et al. 2016) or eyelid closure (Chang, et al. 2016; Wang, et al. 2016) can provide an independent physiological index of these fluctuations. Methods have also been proposed which estimate levels of arousal directly from fMRI data (Haimovici, et al. 2017; Tagliazucchi and Laufs 2014). Whether fluctuations in arousal are an interesting source of neural variation ultimately depends on the specific research question.

There is currently no consensus on the optimal way to account for the effects of fluctuations in arousal in the context of TVC analyses. One relatively simple approach which has been used with success in studies of static FC is to discard time-points during which participants are asleep or have very low arousal (Wang, et al. 2017). However, as mentioned above, censoring strategies are often undesirable for studies of TVC, as they disrupt the spacing and ordering of volumes and preclude certain types of TVC analyses. Instead, the influence of fluctuating arousal can be dealt with statistically by regressing out continuous measures of arousal (such as those mentioned in the previous paragraph). While careful experimental design (e.g. real-time vigilance monitoring) and the use of statistical models can be used to try and minimize the effects of sleep and arousal, doing so is often non-trivial as one needs a very well-articulated model of the contribution of the confounding sources in order to account for them. More work is needed to further characterize the impact of arousal on BOLD TVC and to identify effective strategies to account for these effects.

Finally, we emphasize that there is an inherent trade-off when attempting to remove the influence of arousal on BOLD TVC: These processing steps may very likely remove interesting signal along with putative sources of noise (Pfaff, et al. 2012), as cognitive processes are often intricately linked with arousal and other physiological states. It will be important for future work in the field to appropriately disambiguate the arousal-related signatures that are either detrimental to or facilitative of cognitive performance, thus refining our understanding of the building blocks of the brain's cognitive architecture.

7. What can we conclude, and how should we think about resting BOLD TVC?

Given the evidence we have reviewed, what conclusions can we draw regarding the three questions posed at the beginning of this article? First, we believe that when applied to properly cleaned data, a diverse landscape of analytic and modeling approaches are capable of reliably estimating TVC from BOLD rfMRI time series. As to whether estimates of time-resolved connectivity during rest truly vary in time, we emphasize that the space of "dynamic" phenomena is large,

and that the answer to this question depends critically on selecting appropriate time series features and null models for the specific hypothesis being tested. Second, a robust literature on the physiological basis of static BOLD FC and TVC suggests that these phenomena result in large part from inter-regional synchronization of neural activity, and that patterns of synchronization can be modulated by level of arousal. Third, there is a broad consensus that external task demands can modulate patterns of BOLD FC, and growing evidence that TVC fluctuations during rest are not only reliable within and across individuals, but relevant to ongoing cognition and behavior.

Beyond the questions that inspired this review, it is worth taking a step back and considering how TVC phenomena relate to traditional static FC. How should we think about the transient patterns of FC identified by TVC methods? It seems likely that we should expect to see both similarities and differences relative to patterns of static FC. We might expect similarities based on evidence that static FC states often represent behaviorally relevant network configurations, and it is reasonable to expect that these same configurations may be briefly recapitulated at faster timescales. We may expect to see differences because given FC that varies in time, patterns of static FC will essentially capture some aggregate measure of the strength of a connection over the window in which static FC is calculated. Like any summary measure, these aggregate static FC estimates will likely fail to capture some aspects of the underlying TVC phenomena.

This is an important point, because it can potentially help address the paradox of FC stability discussed in Section 5.2.3: Given that patterns of static FC are so similar across a wide range of behavioral states, why should we expect to see fluctuations in FC during periods of rest when overt behavior remains unchanged? The key to resolving this paradox may involve the recognition that a given value of a summary measure can be realized by multiple different arrangements of the underlying data. In the context of FC, this means that the same pattern of static FC may result from different spatiotemporal patterns of underlying TVC. Further, because TVC fluctuations unfold over time in a particular order, the same distribution of TVC patterns (e.g. 4 TRs in pattern A, 4 TRs in pattern B) can have very different temporal profiles (e.g. ABABABAB, AAAABBBB, AABBAABB, etc.). Brain dynamics unfold over time in a particular sequence, and it is therefore important to go beyond simply identifying FC patterns at high temporal resolution: to further our understanding of brain dynamics, cognition and behavior, we must also consider the temporal aspects of TVC fluctuations (e.g. transition probabilities, dwell times, switching rates). It is not enough to know *what* FC patterns occur, but also *when*. This idea features prominently in recent work on the temporal profiles ("meta-states") of TVC during rest (Vidaurre, et al. 2017b), and how these profiles differ between wake and sleep (Damaraju, et al. 2018; Stevner, et al. 2019). From this perspective, there may be no paradox at all: fluctuations in TVC are not necessarily inconsistent with highly stable patterns of static FC.

8. Advancing the field: Recommendations for moving forward

It is our hope that this paper can serve as not only a review of the current state of the field, but also as a blueprint for future work. TVC analyses of BOLD fMRI and other types of neuroimaging data have the potential to help answer some of the most compelling open questions in cognitive and systems neuroscience. TVC analyses of intrinsic brain activity recorded at rest are fast becoming a key tool for researchers seeking to identify fundamental principles of macro-scale brain dynamics, their spatial and temporal organization, and their relationship to underlying anatomy. Studies of resting TVC have also begun to shed light on disordered intrinsic brain dynamics in individuals with psychiatric and neurological illness, and careful experiments using online measures and naturalistic paradigms promise to reveal fine-grained relationships between patterns of functional connectivity and cognitive, behavioral, and physiological states. At the same time, important questions remain unresolved. How much variance in resting TVC estimates is explainable by various contributing factors (e.g. neural signaling, bodily physiology, cognitive state, head motion)? Precisely how sensitive is BOLD TVC to shifts in cognition? Can we resolve "spontaneous" changes in mental content (e.g. thinking about a cow vs. a horse), or are we limited to studying more general changes in cognitive state (e.g. goal directed future planning vs. undirected mind wandering)? Success in answering these questions will require contributions from and collaboration between researchers with a wide range of backgrounds and perspectives. With this in mind, we offer the following concrete recommendations aimed at facilitating a consensus approach for research into time-varying connectivity.

First, we urge researchers undertaking TVC analyses to carefully consider their choice of terminology when describing their methods and framing their results. Inconsistencies in definitions between researchers have the potential to needlessly muddy an already complicated scientific landscape. While we have proposed the term "time-varying connectivity" as an appropriately broad label, we recognize that debates about the application of this and other terms are likely to continue. As the field evolves, the terminology will undoubtedly continue to expand along with it. This

underscores the importance of ensuring we are clear about our terms and definitions, and that we consider their use in the context of existing terminology.

Second, while TVC methods provide an opportunity to address many interesting questions, they must be carefully applied. Care must be taken in preprocessing and the selection of the appropriate analytic approaches and null models. Findings should be appropriately contextualized against the backdrop of potentially conflicting evidence regarding the validity and reliability of BOLD TVC methods. Experimentalists, theorists, and quantitative methodologists must continue to work together to identify and communicate best practices to help ensure a reliable and useful literature on BOLD TVC. We encourage those new to TVC analyses to take the time to learn and understand the peculiarities and pitfalls of these methods, and to engage in discussions with domain experts to ensure that their findings are robust.

Third, we propose that future work on BOLD TVC be considered from the perspective of the three key questions we outline at the beginning of this article. While the questions we raise are essentially sequential (e.g., there's little value in considering the biological basis of TVC if we conclude that resting BOLD data does not contain TVC in the first place), we recognize that science rarely proceeds in an orderly fashion. As such, it is critical that studies exploring the "latter" questions make clear on which untested or controversial assumptions they rest (e.g. that resting BOLD data exhibit TVC, are the result of underlying neural dynamics, etc.).

As the field continues to move forward, the study of resting brain dynamics will benefit from both the refinement of existing TVC methodologies as well as the use and development of complementary techniques. For example, methods capable of recovering the hemodynamic response function from rfMRI data promise to further elucidate the relationship between neural activity at rest and the observed BOLD signal. This knowledge can in turn help inform the development of models which facilitate the estimation of time-varying directed or "effective" connectivity. As our tools and analyses continue to develop, it will also be critical to assess the impact of data quality and quantity (e.g. scan sequence parameters, scan duration, number of participants) on individual and group-average TVC estimates.

Overall, we believe that statistically rigorous, well validated studies of resting BOLD TVC have the potential to greatly expand our understanding of brain dynamics and their relationship to cognition in health and disease, and that collaborative, open work towards resolving outstanding controversies is the most effective and productive path forward for our field.

Box 1: A brief history of studying the brain at rest

Studying the brain at rest is not a new idea. Scientists have been interested in the dynamics of resting cognition at least since the writings of William James in the late 1800s (James 1890), and much of Hans Berger's pioneering EEG research in the 1920s was focused on the properties of intrinsic brain activity (Karbowski 1990). Following the development of PET and BOLD fMRI in the 1980s and '90s, human functional neuroimaging was initially dominated by task activation paradigms. However, researchers quickly began to notice a set of regions that consistently deactivated in response to external task demands, and which exhibited high metabolic activity during rest. This set of regions was named the default mode network "DMN" in a seminal 2001 paper by Raichle and colleagues (Raichle, et al. 2001). In a complementary line of work, Biswal et al. estimated BOLD fMRI functional connectivity between primary motor cortex and other brain areas, independent of any overt task (Biswal, et al. 1995). The resulting spatial patterns of FC mirrored patterns of activation seen when subjects executed a motor response. These and other findings led to renewed interest in the study of the brain at rest, with the hope that better characterizing "resting state" FC networks would reveal core features of the brain's functional organization.

Neuroimaging studies of the brain at rest quickly converged on a set of canonical FC networks which are consistently observed at rest and correspond with patterns of task-evoked activation and connectivity (Calhoun, et al. 2008; Damoiseaux, et al. 2006; Smith, et al. 2009). While early studies focused on investigating the connectivity of individual networks (e.g. DMN (Greicius, et al. 2003)), this work eventually expanded into efforts to investigate global functional organization by mapping connectivity patterns across the whole brain (e.g. (Yeo, et al. 2011)). These initial observations have been widely replicated across hundreds of studies using a variety of analytic methods (e.g. seed-based connectivity, ICA, community detection).

Inter-individual differences in resting FC patterns have been associated with a wide range of phenotypic traits (e.g. working memory and executive control (Cole, et al. 2012; Hampson, et al. 2006)) and clinical conditions (e.g. psychiatric and neurological disorders (Fox and Greicius 2010; Greicius 2008)), and can be used to predict behavioral performance (e.g. (Rosenberg, et al. 2016)) and individual identity (e.g. (Finn, et al. 2015)).

Despite the success of the resting FC research program in expanding our understanding of human brain function, it has historically been limited by the use of methods that are unable to address fundamental motivating questions about inherently dynamic cognitive and neural process. In response to this limitation, the past decade has seen the emergence of new tools for studying the time-varying properties of the brain at rest.

Box 2: The Elusive Concept of Dynamic Functional Connectivity

The term "dynamic connectivity" has been used to refer to a wide range of approaches for studying time-varying aspects of brain function. These approaches differ in the insights they offer into brain dynamics, and it is important to distinguish what inferences can (and cannot) be made from a particular analysis or model. Below, we briefly outline how four broad classes of TVC methods can be used to expand our understanding of the brain.

Time-resolved estimates of functional connectivity: Empirical estimates of time-resolved connectivity allow scientists to explore how the strength of inter-regional coupling varies over time. These estimates form the basis of empirical studies of TVC. In their most basic form (i.e. time-resolved correlations), they can provide insight into the trajectories by which static ("time-averaged") FC is realized. Time-resolved estimates also allow for fine-grained evaluations of the relationship between FC and ongoing cognition, as well as how summary measures (e.g. variability of FC) may be related to phenotypic traits in health and disease.

Models of brain states and transitions: Many empirical studies of TVC also seek to estimate momentary "brain states" and their transitions. In this paradigm, each state describes a different pattern of whole-brain connectivity. Different models impose varying constraints on the estimated states, such as whether they manifest in isolation (one state per time point) or combination (a mix of states at each time point). The dynamics of these brain states (e.g. time spent in each state, the probability of transitioning between states) can provide a detailed portrait of how functional relationships reorganize through time. Formal model selection and comparison (e.g. using information-theoretic criteria) allows for the evaluation of which models best describe the observed data, and thus permit adjudication of competing hypotheses about data-generating processes.

Comparison to surrogate (null) data: Insight into the dynamical properties of a system can also be achieved by comparing observed data to surrogate data which lack a particular statistical feature of interest. For example, one can generate surrogate "null" time series which have the same low order features as empirical data (e.g. mean, variance, spatiotemporal correlation structure) but lack a higher order feature proposed to exist in the real data (e.g. switching dynamics). The strength of this approach is that it draws from a rich existing literature on time series analysis and enables testing of specific hypotheses about the dynamical properties of an observed time series. Care must be taken to ensure that the tests undertaken are sufficiently narrow and are interpreted as such. For example, claims should be made about the presence or absence of a particular statistical feature rather than "dynamic" FC in general, as "dynamic" phenomena can exist under a wide range of conditions.

Modeling of nonlinear brain dynamics: Unlike the three approaches above which begin with empirically measured BOLD data, it is also possible to instead begin the study of TVC by constructing a detailed biophysical model of the underlying processes give rise to TVC. With appropriate model fitting and tuning, it is possible to invert the observed data into a generative model, and then study the complex (fast timescale) dynamical properties of that model which would normally be obscured by the measurement process. Having established a model of the dynamical processes underlying the observed data, researchers can undertake detailed mechanistic investigations of complex neural dynamics and their relationship to BOLD TVC.

Acknowledgements

We would like to thank Cesar Caballero-Gaudes, Peter Fransson, Lucina Uddin, Sepideh Sadaghiani, Daniele Marinazzo, and Ioannis Pappas for their comments and suggestions on earlier versions of this manuscript. We also thank Abraham Snyder, Jean-Baptiste Poline, Ted Satterthwaite, Caterina Gratton, and Nico Dosenbach for their participation in the discussion which inspired us to write this review.

- DJL was supported the National Science Foundation Graduate Research Fellowship under Grant No. DGE 1106400.
- D. Kessler was supported by NSF grant DMS-1646108.
- DSB acknowledges support from the John D. and Catherine T. MacArthur Foundation, the Alfred P. Sloan Foundation, the ISI Foundation, the Paul Allen Foundation, the Army Research Laboratory (W911NF-10-2-0022), the Army Research Office (Bassett-W911NF-14-1-0679, Grafton-W911NF-16-1-0474, DCIST-W911NF-17-2-0181), the Office of

Naval Research, the National Institute of Mental Health (2-R01-DC-009209-11, R01-MH112847, R01-MH107235, R21-M MH-106799), the National Institute of Child Health and Human Development (1R01HD086888-01), National Institute of Neurological Disorders and Stroke (R01 NS099348), and the National Science Foundation (BCS-1441502, BCS-1430087, NSF PHY-1554488 and BCS-1631550).

- RFB was supported by the Indiana University Office of the Vice President for Research Emerging Area of Research Initiative, Learning: Brains, Machines, and Children.
- MB was supported by the National Health and Medical Research Council (118153, 10371296, 1095227) and the Australian Research Council (CE140100007).
- SK was supported by NIH R01MH111416, R01NS078095, and NSF BCS INSPIRE 1533260.
- AK was supported by a Banting Fellowship from the Canadian Institutes of Health Research.
- RL was supported by a CHIST-ERA IVAN project (20CH21 174081).
- MAL was supported by grants R01 EB016061 and R01 EB026549 from the National Institute of Biomedical Imaging and Bioengineering.
- JMS was supported by the National Health and Medical Research Council (GNT1072403 and GNT1156536).
- WHT was supported by the Knut and Alice Wallenberg Foundation, grant no. 2016.0473.
- LD was supported by a Branco Weiss Fellowship from Society in Science and a Veni grant (016.146.086) from the Dutch Organization for Scientific Research (NWO).
- AR is funded by the Australian Research Council Discovery Early Career Research Award (DECRA, DE170100128) and the Wellcome Trust UK.
- D. Kraft was supported by the German Research Foundation (CRC 1193 grant no. INST 247/859-1).
- MM was supported by grants from the German research foundation SFB CRC-1193 and SFB CRC-TR-128.
- VDC was supported by grants from the National Institutes of Health (R01EB020407, P20GM103472, P30GM122734) and the National Science Foundation (1539067).

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Table 1: Glossary of terms related to BOLD TVC

Term	Definition
functional connectivity (FC)	Statistical dependencies among neurophysiological time series derived from regions or networks. Most often estimated as a correlation coefficient.
static functional connectivity	An estimate of statistical dependence made under assumption that the dependence structure does not vary as a function of time.
statistical stationarity	A formal definition of certain statistical properties being invariant to a shift in time. In practice, stationarity can only be assessed given multiple realizations of a time series (rather than for a single dataset). - Strong stationarity: The probability distribution of the time series is invariant under a shift in time. - Weak stationarity (or second-order stationarity): The mean and covariance of the time series are finite and invariant under a shift in time. This is the definition most time series models use in practice.
time-varying functional connectivity (TVC)	Functional connectivity that varies as a function of time. Also referred to as "dynamic connectivity".
brain state	A transient pattern of whole-brain connectivity. Usually identified by analytic techniques that attempt to model the full repertoire of brain connectivity patterns as being made up of a relatively small number of brain states (often referred to in shorthand simply as "states"). Some of these low-dimensional models constrain the brain to be in a single state at a time, whereas others permit each time point to be a mixture of states.
windowed connectivity	Connectivity estimated over a defined time window that is shorter than the full time series. Windowing can involve weighting or tapering. "Sliding window" methods can be used to produce time-resolved estimates of functional connectivity (one for each window).
dynamical system	A system composed of interacting components (neurons, brain regions, etc.) whose state evolves forward in time according to a particular rule (such as a difference or differential equation). Such systems yield complex behaviors that can be observed via an (often indirect) measurement process.
Hidden Markov Model (HMM)	Statistical model wherein observed data is assumed to be generated from a process that is moving among unobserved states. Fitting an HMM involves estimating (1) properties of each state, (2) transition probabilities between the states, (3) which state is active at each time point. For TVC applications, each state might correspond to a distinct pattern of brain connectivity, the transition probabilities would explain how the brain moves from one state to another, and the estimates of active states would give time-resolved estimates of which state was active at each time point.

Table 2: Key papers on resting BOLD TVC

A method for evaluating dynamic functional network connectivity and task-modulation: application to schizophrenia *Sakoglu et al., 2010;* https://doi.org/10.1007/s10334-010-0197-8 **Time–frequency dynamics of resting-state brain connectivity measured with fMRI** *Chang et al., 2010;* https://doi.org/10.1016/j.neuroimage.2009.12.011 Published almost simultaneously, these two papers were among the first to apply sliding-window and time-frequency analyses to the study of BOLD TVC.
Tracking Whole-Brain Connectivity Dynamics in the Resting State *Allen et al., 2012;* https://doi.org/10.1093/cercor/bhs352 One of the first papers to combine sliding-window analysis and clustering to estimate brain states and study their dynamics.
Resting-state networks show dynamic functional connectivity in awake humans and anesthetized macaques *Hutchison et al., 2012;* https://doi.org/10.1002/hbm.22058 One of the first studies to directly investigate the extent to which BOLD TVC may exist independently of ongoing cognition.
Dynamic BOLD functional connectivity in humans and its electrophysiological correlates *Tagliazzuchi et al., 2012;* https://doi.org/10.3389/fnhum.2012.00339 **EEG correlates of time-varying BOLD functional connectivity** *Chang et al., 2013;* https://doi.org/10.1016/j.neuroimage.2013.01.049 Two of the earliest studies to explore the electrophysiological basis of BOLD TVC using simultaneous EEG/fMRI.
Dynamic functional connectivity: Promise, issues, and interpretations *Hutchison et al., 2013;* https://doi.org/10.1016/j.neuroimage.2013.05.079 Important early review of BOLD TVC findings and methods.
Periods of rest in fMRI contain individual spontaneous events which are related to slowly fluctuating spontaneous activity *Petridou et al., 2013;* https://doi.org/10.1002/hbm.21513 **Time-varying functional network information extracted from brief instances of spontaneous brain activity** *Liu and Duyn, 2013;* https://doi.org/10.1073/pnas.1216856110 Two early studies suggesting that BOLD FC may be shaped by the dynamics of transient co-activation patterns (CAPs).
Time-resolved resting-state brain networks *Zalesky et al., 2014;* https://doi.org/10.1073/pnas.1400181111 Early example of how sliding-window BOLD TVC can be combined with graph-theory analyses to investigate dynamic reorganization of brain networks during rest.
Dynamic functional connectivity of the default mode network tracks daydreaming *Kucyi and Davis, 2014;* https://doi.org/10.1016/j.neuroimage.2014.06.044

Early demonstration that BOLD TVC is associated with time-resolved self-reports of ongoing cognition.

The Chronnectome: Time-Varying Connectivity Networks as the Next Frontier in fMRI Data Discovery
Calhoun et al., 2014; https://doi.org/10.1016/j.neuron.2014.10.015

Review of BOLD TVC methods, including an in-depth discussion of approaches which seek to estimate brain states.

Evaluating dynamic bivariate correlations in resting-state fMRI: A comparison study and a new approach
Lindquist et al., 2014; https://doi.org/10.1016/j.neuroimage.2014.06.052

Can sliding-window correlations reveal dynamic functional connectivity in resting-state fMRI?
Hindriks et al., 2015; https://doi.org/10.1016/j.neuroimage.2015.11.055

On spurious and real fluctuations of dynamic functional connectivity during rest
Leonardi and Van De Ville, 2015; https://doi.org/10.1016/j.neuroimage.2014.09.007

Three papers which carefully evaluate the potential pitfalls of sliding-window approaches and emphasize the importance of comparing against null models.

Classification of schizophrenia and bipolar patients using static and dynamic resting-state fMRI brain connectivity
Rashid et al., 2016; https://doi.org/10.1016/j.neuroimage.2016.04.051

One of the first studies to demonstrate the superiority of BOLD TVC over static FC for classifying individuals based on psychiatric diagnosis.

The dynamic functional connectome: State-of-the-art and perspectives
Preti et al., 2016; https://doi.org/10.1016/j.neuroimage.2016.12.061

Detailed review of a wide range of methods for studying BOLD TVC.

Temporal metastates are associated with differential patterns of time-resolved connectivity, network topology, and attention
Shine et al, 2016; https://doi.org/10.1073/pnas.1604898113

A TVC analysis of two large longitudinal single-subject data sets identified replicable temporal "meta states" with distinct network topologies, time-varying properties, and associations with cognition.

On the Stability of BOLD fMRI Correlations
Laumann et al., 2017; https://doi.org/10.1093/cercor/bhw265

Influential paper challenging the notion that resting BOLD TVC is related to ongoing cognition. Argues that resting BOLD is consistent with a stationary model and that resting TVC can largely be explained by sampling variability, head motion, and fluctuations in arousal.

Interpreting temporal fluctuations in resting-state functional connectivity MRI
Liegeois et al, 2017; https://doi.org/10.1016/j.neuroimage.2017.09.012

Detailed exploration of which statistical properties are consistent with "dynamic" FC. Includes a detailed review of the concept of statistical stationarity, as well as an assessment of several common statistical models.

Comparing test-retest reliability of dynamic functional connectivity methods
Choe et al., 2017; https://doi.org/10.1016/j.neuroimage.2017.07.005

Replicability of time-varying connectivity patterns in large resting state fMRI samples
Abrol et al., 2017; https://doi.org/10.1016/j.neuroimage.2017.09.020

Two of the first large, systematic evaluations of the reliability of methods for estimating BOLD TVC and identifying brain states.
Brain network dynamics are hierarchically organized in time *Vidaurre et al., 2017;* https://doi.org/10.1073/pnas.1705120114 HMM analysis reveals a rich hierarchical temporal structure in the pattern of transitions between brain states, and that individual differences in "meta state" occupancy are related to cognition.
Dynamic models of large-scale brain activity *Breakspear, 2017;* https://doi.org/10.1038/nn.4497 Accessible review of methods for modeling large scale brain dynamics. Includes a primer on core concepts from dynamical systems theory.
Neuronal Origin of the Temporal Dynamics of Spontaneous BOLD Activity Correlation *Matsui et al., 2018;* https://doi.org/10.1093/cercor/bhy045 Simultaneous recording of calcium imaging and optical hemodynamics reveal a clear neural basis for BOLD TVC, and that fluctuations in BOLD TVC are related to transient neural CAPs.
Simulations to benchmark time-varying connectivity methods for fMRI *Thompson et al., 2018;* https://doi.org/10.1371/journal.pcbi.1006196 Recent work using multiple simulation strategies to undertake a systematic evaluation of the sensitivity of common TVC methods. Provides an open-source toolbox for simulation and benchmarking.
Putting the "dynamic" back into dynamic functional connectivity *Heitmann and Breakspear, 2018;* https://doi.org/10.1162/netn_a_00041 Application of large-scale modeling to investigate which kinds of neural dynamics may give rise to BOLD TVC. Argues that BOLD TVC likely reflects complex nonlinear and nonstationary neural dynamics.

Appendix: Embracing new forums for scientific discourse

Although it is natural to expect that different scientists may have different interpretations of specific empirical findings and the published literature as a whole, efforts to resolve scientific controversies are ultimately a fool's errand if there can be no agreement (or no clarity) on at least the key terms, open questions, and possible adjudicating experiments. While the scholarly literature on TVC grows richer by the day—and there is no replacement for high quality research outputs—we have found great utility in venues for collaboration and discussion that are more fluid, interactive, and fast-moving than the conventional scientific publication pipeline. Each of these forums have their own unique strengths and weaknesses, but in combination provide an exciting opportunity to facilitate progress on difficult questions in our field and beyond.

Twitter posts and subsequent discussion threads are fantastic for stoking spontaneous, accessible debate among widely distributed researchers. At the same time, these conversations can be challenging to parse after the fact, are difficult to archive, and the arbitrary character constraints often require simplifications that are obfuscating rather than clarifying. Mailing lists trade the spontaneity and real-time interactions of social media for an opportunity to hold conversations in a format that is unconstrained by character limits or the stylistic conventions of journal articles. Their "back-and-forth" structure permits easy archiving and deep, considered dialogue. Offline, conferences offer a unique opportunity for especially meaningful interactions: presentations and the discussions that follow them (including online) afford an opportunity to communicate high-level arguments to a wide audience. We applaud the introduction of panel-style discussions such as those held recently at the 2017 and 2018 Organization for Human Brain Mapping annual meetings. In addition to formal conference sessions, we have seen first-hand the power of ad-hoc in-person discussions to rapidly foster mutual understanding and collaboration on an impressive scale—indeed, this paper is an outgrowth of an open-invitation round-table session organized via Twitter at OHBM 2017.[a] We invite other researchers interested in continuing to advance the discussion around TVC to join our online discussion group. The "Time-Varying Working Group"[b] offers a forum for continued refinement and updating of key theoretical questions along with discussion of the latest empirical findings.

[a] https://twitter.com/danjlurie/status/880201676258332678
[b] https://groups.google.com/forum/#!forum/time-varying-working-group

Supplementary Information:

Publication counts for Figure 1 were determined by searching the NIH PubMed database in early 2019.

The search term for all TVC papers was:

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("dynamic connectivity"[TIAB] OR "dynamic functional connectivity"[TIAB] OR "dynamic FC"[TIAB] OR "connectivity dynamics"[TIAB] OR "FC dynamics"[TIAB] OR "functional network dynamics"[TIAB] OR "FC network dynamics"[TIAB] OR "functional brain network dynamics"[TIAB] OR "time-varying connectivity"[TIAB] OR "time-varying functional connectivity"[TIAB] OR "time-varying FC"[TIAB] OR "time varying connectivity"[TIAB] OR "time varying functional connectivity"[TIAB] OR "time varying FC"[TIAB] OR "time resolved connectivity"[TIAB] OR "time resolved functional connectivity"[TIAB] OR "time resolved FC"[TIAB] OR "time-resolved connectivity"[TIAB] OR "time-resolved functional connectivity"[TIAB] OR "time-resolved FC"[TIAB] OR "dynamic functional network connectivity"[TIAB]) AND ("functional magnetic resonance imaging"[TIAB] OR "functional MRI"[TIAB] OR "fmri"[TIAB])
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The search term for resting TVC papers was:

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("dynamic connectivity"[TIAB] OR "dynamic functional connectivity"[TIAB] OR "dynamic FC"[TIAB] OR "connectivity dynamics"[TIAB] OR "FC dynamics"[TIAB] OR "functional network dynamics"[TIAB] OR "FC network dynamics"[TIAB] OR "functional brain network dynamics"[TIAB] OR "time-varying connectivity"[TIAB] OR "time-varying functional connectivity"[TIAB] OR "time-varying FC"[TIAB] OR "time varying connectivity"[TIAB] OR "time varying functional connectivity"[TIAB] OR "time varying FC"[TIAB] OR "time resolved connectivity"[TIAB] OR "time resolved functional connectivity"[TIAB] OR "time resolved FC"[TIAB] OR "time-resolved connectivity"[TIAB] OR "time-resolved functional connectivity"[TIAB] OR "time-resolved FC"[TIAB] OR "dynamic functional network connectivity"[TIAB]) AND ("functional magnetic resonance imaging"[TIAB] OR "functional MRI"[TIAB] OR "fmri"[TIAB]) AND ("rest"[TIAB] OR "resting"[TIAB] OR "resting-state"[TIAB] OR "intrinsic"[TIAB])
```

Python code for creating Figure 1 and components of Figure 2 can be found at:

https://github.com/danlurie/lurie_kessler_2019