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Neurocognitive biases and the patterns of spontaneous correlations in the human cortex

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When the brain is 'at rest', spatiotemporal activity patterns emerge spontaneously, that is, in the absence of an overt task. However, what these patterns reveal about cortical function remains elusive. In this article, we put forward the hypothesis that the correlation patterns among these spontaneous fluctuations (SPs) reflect the profile of individual *a priori* cognitive biases, coded as synaptic efficacies in cortical networks. Thus, SPs offer a new means for mapping personal traits in both neurotypical and atypical cases. Three sets of observations and related empirical evidence provide support for this hypothesis. First, SPs correspond to activation patterns that occur during typical task performance. Second, individual differences in SPs reflect individual biases and abnormalities. Finally, SPs can be actively remodeled in a long-term manner by focused and intense cortical training.

Spontaneously emerging spatiotemporal neuronal activity patterns

Although most cognitive neuroscience research has traditionally focused on mapping the details of task-induced activation patterns, in recent years it has become evident that brain activity in the absence of such overt tasks is also highly informative. Indeed, following the pioneering observations of Arieli and colleagues in the visual cortex of anesthetized cats [1,2] and Biswal *et al.*'s study of human motor cortex [3], it became clear that even in the absence of a task – that is, in what appears to be a state of rest – the cerebral cortex generates rich and consistent spatiotemporal patterns of activity. In blood oxygen-level-dependent functional MRI (BOLD-fMRI), these spontaneously emerging 'resting-state' activity fluctuations (see Glossary) appear to span the entire cortical mantle and are of similar amplitude to those produced during task performance [4]. Furthermore, these activity patterns have now been docu-

mented in human single unit and local field potential (LFP) recordings as well [5–8], revealing that the dynamics of these spontaneously emerging patterns are far slower than typical task activations [7].

Despite extensive research, the functional role of spontaneous fluctuations remains elusive, although a number of hypotheses have been put forward in an attempt to explain it (Box 1) [9–11]. However, irrespective of the specific functions that spontaneous activity plays in cortical processing, one can ask what kind of information can be deciphered from these spontaneous patterns.

In what follows, extending previous notions about SPs, we propose the hypothesis – termed spontaneous trait reactivation (STR) – that SPs, at least as revealed in the human cortex, could offer a window into the structure of an individual's inner world (i.e., the unique profile of personality traits), tendencies, and even pathologies. More specifically, we propose that in the human cortex the correlation structure or functional connectivity (FC) revealed by spontaneous fluctuations is informative about

Glossary

Connectivity bias: strength or efficacy of excitatory synaptic coupling between two neurons or between neuronal groups.

Default mode/resting state/task negative network: network of brain areas, located in specific regions of medial frontal, parietal, and anterior temporal cortex, whose neuronal activity increases on entering a resting state.

Default/resting state fluctuations: ultra-slow fluctuations in neuronal activity that occur in the absence of an explicit task. These fluctuations emerge in networks across the entire cortex and are not confined to the default mode network. Note that these networks are often referred to as resting-state networks.

Functional connectivity/functional correlation: extent to which the neuronal activity across two brain sites is co-modulated. High functional connectivity may be generated by external sources (e.g., common inputs) and hence does not always imply connectivity biases.

Hebbian learning: fundamental learning rule by which inter-neuronal connectivity biases are strengthened following neuronal correlated activations and weakened if the neuronal activity is de-correlated.

Intrinsic/self-projection network: similar to the default mode network but with the added assumption that this network is specialized for internally oriented, self-related processes.

Ongoing activity: similar to the resting-state fluctuations but includes the assumption that task-related activations are superimposed on top of the spontaneous – and hence ongoing – fluctuations.

Resting state: condition in which an individual is not engaged in any focused and intentional cognitive task.

Spontaneous fluctuations: similar to the resting-state fluctuations, but can also occur during task performance in networks that are not activated by the task.

Spontaneous patterns: matrix of correlation levels generated by spontaneous fluctuations across all cortical sites.

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Box 1. Possible functions of spontaneous (resting state) activity

The possible function of spontaneous activations is still debated. Some of the options that have been proposed are listed below in ascending order of complexity.

- (i) **Vegetative function:** the most straightforward and basic possibility that could account for the spontaneous activity is that neurons simply must emit action potentials in order to survive [94]. Thus, it could be that intrinsic neuronal activation serves a basic vegetative function. Connected to this is the intriguing hypothesis that spontaneous activity, at least during sleep, may play an important function in synaptic regularization or renormalization [95,96].
- (ii) **Keeping cortical networks close to the ignition threshold:** various models have proposed that spontaneous activity may be an unavoidable consequence of the attempt of cortical networks to remain close to the firing threshold, thus allowing quicker response dynamics [97].
- (iii) **Solution exploration:** a possibility derived from attractor network models suggests that noise may serve as a means of arriving at optimal solutions [98]. More generally, spontaneous activity may be viewed as allowing cortical networks to explore a wider range of computational solutions.
- (iv) **Memory and motivationally driven activations:** finally, we cannot rule out the possibility that the spontaneous patterns are not that spontaneous, that is, they may be driven by a chain of internal cognitive events that are opaque to the experimenter and yet are not that different from stimulus-driven activations (see 'Are we aware of the SPs?' section).

the profile of each person's neuronal connectivity biases, which in turn endow the individual with a unique set of personality characteristics and cognitive traits.

Spontaneous trait reactivation and related proposals

The nature of information that can be extracted from SPs was recently addressed by Fiser *et al.*, who suggested that spontaneous fluctuations may be indicative of perceptual priors – as defined within a Bayesian inference framework – that is, a representation of the statistical structure of the external environment [10]. In a similar vein, Sadaghiani and Kleinschmidt more recently proposed that SPs may reflect 'the structure of memory systems modeling the statistical structure of the world' ([12], p. 379).

Here, we extend these notions by hypothesizing that the average (across time) correlation structure of spontaneous fluctuations reflects not only external statistical structures, but also the entire set of individual inner cortical and cognitive biases. Note that the hypothesis concerns the correlation structure of SPs, regardless of the specific dynamics of spontaneous fluctuations. Thus, our proposal does not make any assumptions about the nature of the fluctuations or their function. The basis for our hypothesis is the observation that, despite the highly dynamic and fluctuating nature of spontaneous activations, the matrix of correlations among different cortical sites revealed by spontaneous fluctuations remains remarkably reproducible as long as the system is not perturbed by intense task activation (see below). Our aim is to consider the kind of information that may be contained in these relatively stable correlation patterns.

It should be noted that our hypothesis, emphasizing SPs as informative of the structure of the inner world of human individuals, does not necessarily conflict with the view

implicating SPs as representations of *a priori* information or predictions about the external world [10–12]. Indeed cortical network biases, particularly in early sensory representations, are naturally linked to the statistical regularities of the environment. However, at higher levels of processing, even within the visual system proper, such external environmental priors are integrated with additional parameters, most importantly the intrinsic adaptive value of the information as it pertains to each individual. A clear example of such integration is reflected in the highly expanded nature of human face representations [13,14]. Although it is clear that such representations reflect the statistical properties of faces, their cortical prevalence compared to representations of other physical objects and even the anatomical location [15] of face representations is likely due not only to their external statistical properties but also to the crucial value of faces for human social communication [16]. Furthermore, as we argue below, the connectivity biases of such representations may differ depending on each individual's traits, sensitivities, and, importantly, pathologies.

The importance of connectivity biases in cortical function has been recognized since the seminal work of Hebb [17], who proposed that such biases are embodied in the synaptic efficacies of cortical interneuronal connections [18]. More generally, these connectional tendencies are an essential component in determining individual traits and sensitivities in neurotypical individuals, as well as in those suffering from brain pathologies [19]. Here we review evidence that the SPs may indeed provide an important and unique window into uncovering such network and cognitive biases in individual brains. However, even though *a priori* biases have been amply recognized since the time of von Helmholtz [20] as playing a critical role in numerous cognitive functions from perception to decision-making [21–23], the attempt to link them to spontaneous resting-state fluctuations may appear questionable. Below we discuss the conceptual and experimental motivation for proposing such a link.

A toy model of *a priori* biases

Why should SPs reflect the individual's cortical network biases? To illustrate how the proposed link between these two phenomena comes about, we consider a highly simplified toy model (Figure 1).

We start by considering a simple feed-forward circuit consisting of four V1-like line detectors that feed converging inputs into a target high-order neuron. Three of the neurons in the input layer (red, left) are appropriately positioned to correspond to a triangle shape, whereas the fourth neuron (blue) does not. Now consider that during daily life the system is repeatedly exposed to a triangle shape, leading to common activation of the three red input neurons and the target neuron, but no activation of the blue neuron. Following simple Hebbian learning, we expect the training pattern to generate corresponding modification of synaptic efficacy, essentially embedding a trace of the prior average co-activations in the network connections (red plus signs). Importantly, note that restructuring of the connectivity strength of this simple circuit now endows it with *a priori* sensitivity towards a

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