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The signatures of conscious access and its phenomenology are consistent with large-scale brain communication at criticality

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ABSTRACT

Conscious awareness refers to information processing in the brain that is accompanied by subjective, reportable experiences. Current models of conscious access propose that sufficiently strong sensory stimuli ignite a global network of regions allowing further processing. The immense number of possible experiences indicates that activity associated with conscious awareness must be highly differentiated. However, information must also be integrated to account for the unitary nature of consciousness. We present a computational model that identifies conscious access with self-sustained percolation in an anatomical network. We show that the amount of integrated information (Φ) is maximal at the critical threshold. To the extent that self-sustained percolation relates to conscious access, the model supports a link between information integration and conscious access. We also identify a posterior "hotspot" of regions presenting high levels of information sharing. Finally, competitive activity spreading qualitatively describes the results of paradigms such as backward masking and binocular rivalry.

1. Introduction

Consciousness is both a mystery and a commonplace experience. The most daunting question about consciousness is how a particular portion of matter – the brain – can develop a unique, first-person point of view, phenomenal experiences, and even reflect upon its own nature (Chalmers, 1995). An associated question is why phenomenal experiences feel the way they feel; in other words, what properties of such portion of matter account for the *redness* of red, or the suffering associated with a toothache (Lewis, 1956). Philosophers have battled with these difficult questions (and also among themselves) for centuries, leading to the contemporary consensus that there is indeed something to be explained scientifically about consciousness, and that such explanation is most likely to involve the brain (Dennett, 1993).

The contemporary neuroscience of consciousness builds upon this consensus and adopts the experimental approach of finding the neural correlates of a conscious experience, i.e. the minimal set of events in the brain (presumably the firing of certain neurons) necessary for such a conscious experience to occur. This is the backbone of the research programme proposed by Bachmann (Bachmann, 1984) and afterwards by Crick & Koch in their influential 1990 article (Crick & Koch, 1990). A wealth of experimental data on the neural correlates of different sensory modalities has accumulated since Crick & Koch's seminal proposal, which will not be presented here for reasons of space, but can be read from a number of comprehensive review articles (Bachmann, 2015; Dehaene, 2014; Koch, Massimini, Boly, & Tononi, 2016a). In recent years, a shift has occurred in the research community from the search for neural correlates of consciousness towards the search for models of consciousness (Seth, 2007). A model of consciousness is understood here as a mechanistic (either qualitative or quantitative) explanation of how brain activity leads to conscious awareness. Ideally, models of consciousness must have predictive power, i.e. they should be able to predict from their proposed mechanism what

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the neural correlates of a given conscious experience are.

An influential model of conscious access[1] has been proposed by Baars, Changeux and Dehaene and is commonly referred to as the global workspace model (Baars, 2005; Dehaene & Changeux, 2011; Dehaene, Changeux, & Naccache, 2011; Dehaene, Kerszberg, & Changeux, 1998). Their proponents suggest a competitive mechanism at a neural periphery consisting of parallel processors. A non-linear, all-or-none transition ("ignition") occurs when one of the competing incoming stimuli gains access to a distributed set of neurons comprising the global workspace. Such transition leads to self-sustained activity that can be accessed by different brain processes (e.g. working memory, decision making). The competition to gain access to the global workspace accounts for the results of several psychophysical experiments, such as backward masking and binocular rivalry – i.e. for a short time after its ignition by a given stimulus, the global workspace remains inaccessible to other stimuli (Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006). Neuroimaging experiments have consistently identified the global workspace with the fronto-parietal cortex of the brain (for an example, see Carmel, Lavie, & Rees, 2006; further examples are discussed in the references on the neural correlates of consciousness). Thus, it can be said that the global workspace model is one of conscious access: it posits that the function of conscious awareness is the broadcasting of information in the brain, and suggests a plausible neuronal mechanism for such broadcasting.

Other models of consciousness address instead the phenomenology of consciousness. The information integration theory put forward by Giulio Tononi identifies the properties that a physical system should have in order to present a high level of differentiation, as well as of information integration. Differentiation relates to the phenomenal experience of the uniqueness of any conscious event, each a single one among an astronomical number of possibilities. While differentiation is maximized by statistically independent neuronal firing, the unitary nature of each conscious experience suggests that information integration is another key physical mechanism underlying conscious phenomenology. From these considerations, Tononi and colleagues have derived a series of mathematical procedures to quantify the level of information integration in an arbitrary physical system (Φ) (Tononi, 2004; Tononi, 2011; Tononi, Boly, Massimini, & Koch, 2016). While generally intractable, heuristics and approximations have been employed to support the theory (Barrett & Seth, 2011; Sasai, Boly, Mensen, & Tononi, 2016). It is nevertheless important to remark that while a high value of Φ is proposed as indicative of consciousness in a given physical system, the theory does not necessarily specify the mechanisms that generate such value of Φ.

This description of both models suggests that the global workspace theory and the information integration theory address two different aspects of the conscious experience: the first tackles the issue of conscious access (closely related to the function of conscious awareness), while the second the phenomenology of consciousness. The objective of the present work is to propose a mechanism based on the global workspace model that is compatible with the proposal that high values of Φ are indicative of conscious awareness. In doing so, we also put forward a mechanism based on simple physical principles by virtue of which a system can attain high values of Φ. In other words; we aim to show that both theories are compatible when considered as theories of conscious access and the phenomenology of consciousness, respectively.

The mechanism we propose to fulfill our objective is the propagation of information in the brain at the "edge of failure", i.e. at the critical point at which activity becomes self-sustained (Haimovici, Tagliazucchi, Balenzuela, & Chialvo, 2013). This mechanism is similar to that proposed by a class of mathematical models of the cerebral cortex known as neuropercolation models (Kozma, 2007). As we will discuss extensively below, there is empirical evidence supporting critical-like dynamics in the human brain, adding experimental plausibility to the proposed mechanism (Chialvo, 2010). We develop a conceptual computational model incorporating realistic anatomical connectivity to test the feasibility of our hypothesis, and then discuss the relationship between our results and more neurobiologically realistic models.

2. Materials and methods

2.1. Anatomical connectivity network

As part of our computational model we employ an anatomical connectivity network of the cerebral cortex inferred from diffusion tensor imaging (DSI) data from 5 healthy participants (mean age 29.4 years, all male) (the "anatomical connectome") (Hagmann et al., 2008). The network comprises 998 regions of interest (each 1.5 cm^2 in area) placed throughout the cortex (but excluding subcortical structures and the cerebellum) of individual participants, being later mapped into a common space. White matter tractography was applied to compute fiber trajectories and to construct a network by linking every two nodes for which a fiber existed starting in one and ending in the other. A network representation was obtained by averaging the fiber densities between nodes of all participants. The weighted adjacency matrix of this average network is noted as W_{ij}.

The topological properties of the anatomical connectivity network are described in Hagmann et al., 2008. Briefly, the distribution of strengths (i.e. the total weight of connections attached to a node) follows an exponential distribution, and the nodes with the highest strength (as well as other measures of network centrality) are located within a "structural core" comprising the precuneus, the posterior cingulate cortex and, to a lesser degree, parietal and frontal brain regions.

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[1] In this work, "conscious access" refers to the functionalist or psychological perspective on consciousness. "Conscious phenomenology" refers to the subjective, first-person qualities of consciousness (see the discussion in Chalmers, 1996, for further clarification on this distinction). "Conscious awareness" is more loosely employed to refer to conscious access and the associated phenomenology going hand by hand (but see Block, 2005). Finally, "conscious state" refers to a state in which conscious awareness can occur (e.g. wakefulness as opposed to the comatose state), which is not necessarily disentangled from conscious content itself (Bachmann & Hudetz, 2014).