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Breakdown of long-range temporal correlations in brain oscillations during general anesthesia

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ABSTRACT

Consciousness has been hypothesized to emerge from complex neuronal dynamics, which prevails when brain operates in a critical state. Evidence supporting this hypothesis comes mainly from studies investigating neuronal activity on a short time-scale of seconds. However, a key aspect of criticality is presence of scale-free temporal dependencies occurring across a wide range of time-scales. Indeed, robust long-range temporal correlations (LRTCs) are found in neuronal oscillations during conscious states, but it is not known how LRTCs are affected by loss of consciousness. To further test a relation between critical dynamics and consciousness, we investigated LRTCs in electrocorticography signals recorded from four macaque monkeys during resting wakefulness and general anesthesia induced by various anesthetics (ketamine, medetomidine, or propofol). Detrended Fluctuation Analysis was used to estimate LRTCs in amplitude fluctuations (envelopes) of band-pass filtered signals. We demonstrate two main findings. First, during conscious states all lateral cortical regions are characterized by significant LRTCs of alpha-band activity (7-14 Hz). LRTCs are stronger in the eyes-open than eyes-closed state, but in both states they form a spatial gradient, with anterior brain regions exhibiting stronger LRTCs than posterior regions. Second, we observed a substantial decrease of LRTCs during loss of consciousness, the magnitude of which was associated with the baseline (i.e. pre-anesthesia) state of the brain. Specifically, brain regions characterized by strongest LRTCs during a wakeful baseline exhibited greatest decreases during anesthesia (i.e. "the rich got poorer"), which consequently disturbed the posterior-anterior gradient. Therefore, our results suggest that general anesthesia affects mainly brain areas characterized by strongest LRTCs during wakefulness, which might account for lack of capacities for extensive temporal integration during loss of consciousness.

law scaling (Beggs and Timme, 2012).

1. Introduction

Brain activity, both task-related and spontaneously generated, is characterized by complex spatio-temporal dynamics. It has been proposed that understanding brain as a system operating in a critical state might provide a theoretical framework allowing comprehensive description of neuronal activity (review: Chialvo, 2007, 2010; Shew and Plenz, 2013; Beggs and Timme, 2012). A critical state can occur in complex systems composed of multiple interacting elements. When balanced interactions among the elements keep a system operating at the verge of order and randomness a plethora of non-trivial features can be observed (in contrast to rather trivial states of complete order and randomness). A hallmark of criticality is lack of any characteristic scale in system's activity (i.e. scale-free dynamics), which is indicated by a power-

First evidence for brain operating in a critical state came from studies investigating "neuronal avalanches", which were defined as temporally consistent bursts (clusters) of activations occurring simultaneously at several brain locations. Neuronal avalanches were first investigated in LFP recordings, with activations defined based on deflections of LFP signals. Scale-free avalanches, with their size and duration following a power law, were observed both in vitro (Beggs and Plenz, 2003, 2004) and in vivo (Gireesh and Plenz, 2008; Petermann et al., 2009; Hahn et al., 2010). Further studies confirmed that similar scale-free dynamics can be found in avalanches defined based on non-invasively recorded MEG (Shriki et al., 2013) or fMRI data (He, 2011; Tagliazucchi et al., 2012).

But evidence for brain criticality is not limited to studies investigating "neuronal avalanches". Another line of research focused on long-range

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Abbreviations: ECoG, electrocorticography; LRTCs, long-range temporal correlations; DFA, detrended fluctuations analysis; TRF, temporal receptive field; EO, eyes open; EC, eyes closed. * Corresponding author. Laboratory of Brain Imaging, Neurobiology Center, Nencki Institute of Experimental Biology of Polish Academy of Sciences, 3 Pasteura Str., 02-093 Warsaw, Poland.

temporal correlations (LRTCs), which are defined as a power-law decay of an autocorrelation function and thus indicate that a signal exhibits scale-free patterns in the temporal domain (in the form of 1/*f* spectrum). LRTCs can be thought to reflect a long "memory" of a signal and a simultaneous modulation across a range of time-scales. Robust LRTCs were found in amplitude modulation of oscillatory brain activity (Linkenkaer-Hansen et al., 2001, 2004) and in temporal progression of EEG topographical voltage patterns (so called "microstates"; Van de Ville et al., 2010; Gschwind et al., 2015). Importantly, even before describing LRTCs in brain activity, their presence had been observed in behavioral patterns of humans and other species (Gilden et al., 1995; Kello et al., 2010). Recent studies demonstrate links between these various scales of analysis by showing that LRTCs in neuronal oscillations (meso-scale) are related to "neuronal avalanches" in spiking activity (micro-scale; Poil et al., 2012) and, at the same time, to temporal dependencies observed in behavior (macro-scale; Palva et al., 2013; Smit et al., 2013).

Operating in a critical regime provides functional benefits for a system, as it allows balanced propagation of external and internal perturbations and is related to maximization of information storage and transfer (Shew et al., 2009, 2011; Marinazzo et al., 2014). Crucially, the



Fig. 1. Long-range temporal correlations in brain oscillations during wakefulness and anesthesia. (**A**) Brain electrocorticographic activity representative for two conditions: pre-anesthesia eyes-closed baseline (*pre-EC*) and general anesthesia (*ANES*). Upper panels show fragments of broadband (non-filtered) voltage traces (in gray), whereas in the lower panels alpha-band voltage traces (after band-pass filtering) and amplitude envelopes (in blue) are presented. (**B**) Fluctuation functions, showing how variance of the envelopes scales across windows of different lengths (i.e. time-scales), plotted in log-log coordinates. Linear regression is performed and the slope of the fitted straight line (in red) defines the DFA scaling exponent. To obtain a reliable estimate of the exponent only the data-points (windows) marked in red were used for linear regression, as the narrow windows inherently exhibit a steeper scaling (lower left corner; see methods), whereas for the widest windows there was not enough data to reliably estimate the variability (high variability in the upper right corner). (**C**) Topographic maps of the DFA scaling exponent. Signals and fluctuation functions presented in panels A and B, respectively, were estimated from an electrode marked by a black circle. Presented data are from a session number C7 (monkey: Chibi, anesthetic: KTMD).

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