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Discussion

The aim of this thesis was to understand the mechanism and functional role of scale-free neuronal oscillations within the framework of critical-state dynamics. In Chapter 1, I gave an overview of the methods and findings regarding the scale-free nature of neuronal oscillations. In Chapter 2, I modelled scale-free neuronal oscillations using a computer model of a neuronal network. This model gave the first link between two different measures of scale-free dynamics—neuronal avalanches and long-range temporal correlations (LRTC) of oscillations—by showing that they can co-emerge through a balance of excitatory and inhibitory connectivity. This is a previously undescribed form of neuronal network dynamics, *multi-level criticality*, with spatial scale-free spreading of activity on short-time scales (<100 ms) and scale-free temporal amplitude modulation of oscillations on long time-scales (>2 seconds). In Chapter 3, I found that networks exhibiting multi-level criticality optimized three important stimulus-related functions of neuronal networks; the post-stimulus phase locking is regulated by the phase and amplitude of ongoing network oscillations, and the range of stimulus strengths over which a network can give differential responses is largest. This suggests that multi-level criticality optimizes the versatility of neuronal network function, and that the functional role of oscillations is determined by the criticality of a network. Finally, in Chapter 4, I investigated the relationship between oscillations and excitation-inhibition ratio (E/I). I showed that the oscillation amplitude and LRTC were strongly coupled, and that this coupling could be used to estimate E/I of a network. This novel observation led to a new biomarker, $\widehat{E/I}$, for use in *in vivo* recordings. The model also predicted that post-stimulus phase-locking response to a stimulus was dependent on E/I of a network. We tested these results in human magnetoencephalography (MEG) recordings, where subjects performed a threshold stimulus detection task, and found that the human cortex can support a range of $\widehat{E/I}$ from inhibition dominated to excitation dominated and that $\widehat{E/I}$ could account for inter-subject variability in phase-locking response.

Critical-state dynamics of neuronal oscillations

Since the discovery of scale-free neuronal oscillations (Linkenkaer-Hansen et al. 2001) evidence has mounted for their importance in neuronal network function (Chapter 1). Studies have found that LRTC are correlated with fluctuations in human performance (Smit et al. 2013; Palva et al. 2013), and are disrupted in multiple disorders (Linkenkaer-Hansen et al. 2005; Montez et al. 2009; Nikulin et al. 2012). However, without a model to be able to systematically alter LRTC it was difficult to determine the mechanism of LRTC, and its relationship to critical-state dynamics. By designing the critical oscillations (CROS) model we were able to show that as network E/I is increased the network dynamics go through a phase-transition from an ordered weakly-oscillating phase to a disordered strongly-oscillating phase as expected from the framework of critical-state dynamics (Chapter 2). LRTC are maximized at the critical point between these two phases. We also found that shifts in LRTC are paralleled by changes in neuronal avalanche dynamics providing further support for LRTC being a critical phenomenon.

It still remains to be seen whether this critical point can be self-organizing (Bak et al. 1987), for which developmental changes in neuronal connectivity (Sporns et al. 2004) or plasticity (Turrigiano and Nelson 2004) mechanisms would regulate the network towards the required E/I balance. The model studied in the thesis has a fixed topology and it will be interesting to investigate how different forms of topology (Bullmore and Sporns 2012) are able to support multi-level criticality. It is likely that E/I ratio is not the sole determinant of critical dynamics with network topology also playing a role. Previous models have produced neuronal avalanches, but have not reported LRTC of oscillations (Shew et al. 2009; Kinouchi and Copelli 2006; Levina et al. 2007; Millman et al. 2010). I propose that E/I balance is necessary but not sufficient for multi-level criticality, and that other aspects including topology of network, size of network, and the synaptic dynamics of neurons are necessary for oscillatory criticality to occur.

Integrating different measures of neuronal activity

Different measures of neuronal activity have shown scale-free dynamics (Chialvo 2010) including neuronal avalanches (Beggs and Plenz 2003; Petermann et al. 2009; Arviv et al. 2015), LRTC of band-pass filtered oscillations (Linkenkaer-Hansen et al. 2001), broadband scaling of FMRI and EEG recordings (He et al. 2010) and correlation structure in resting-state FMRI recordings (Fraiman and Chialvo 2012). However, it has not been clear how to link these different measures into a common framework. In Chapter 2, we discovered a link between neuronal avalanches and LRTC of oscillations, which has since been supported by experimental evidence where correlations have been found between these two measures of scale-free activity in human MEG and iEEG recordings (Palva et al. 2013; Zhigalov et al. 2015).

In Chapter 3, we show that the level of criticality controls evoked oscillatory responses. By integrating these different measures, we allow comparisons to be made between studies using these methods, and can offer plausible reasons for contradictions in the literature. Characterizing mass-neuronal activity is a field that has rapidly expanded since Hans Berger first recorded EEG (Berger 1929), in terms of recording (MEG, FMRI, optical imaging, invasive electrode recordings) and analysis techniques (spectral, connectivity, non-linear, rest vs. task-evoked). This had led to difficulties in reconciling how different experimental findings in neuronal activity leads to perceptions and behaviors. With the mass of data coming from all these results, models are urgently required that can integrate these different measurements (Sotero and Trujillo-Barreto 2008; Markram et al. 2011), and I propose that without the elements of the model exhibiting critical-state dynamics they will not be able to reproduce the variability that is found empirically in neuronal signals.

Functions of critical-state dynamics

One of the major reasons given for why neuronal networks would self-organize to the critical state is the purported functional capabilities in this state (Shew and Plenz 2013). In terms of neuronal avalanches it has been shown that criticality maximizes the information

content of avalanches (Shew et al. 2011), and dynamic range of response to stimuli (Kinouchi and Copelli 2006; Shew et al. 2009). In Chapter 3, I show that functions of neuronal networks that have been assigned to neuronal oscillations are also optimal in the critical state. Pre-stimulus regulation of post-stimulus response has emerged as an important measure to explain fluctuations in human task performance (Linkenkaer-Hansen et al. 2004; Jensen et al. 2012), and we show that this ability is controlled through critical-state dynamics.

It has yet to be determined how other functions that have been assigned to neuronal oscillations are related to the criticality of the oscillations (Buzsaki 2006). Neuronal oscillations in different cortical areas are commonly analyzed for their ability to synchronize their phases with each other (Gray et al. 1989; Nikouline et al. 2001; Varela et al. 2001; Melloni et al. 2007). Long-distance phase synchrony of alpha/beta oscillations in frontal and parietal regions correlate with cognitive functions. The phase synchrony was sustained and stable during the retention interval of working memory tasks (Palva et al. 2010), it was reduced in a visual perception task in schizophrenia (Uhlhaas and Singer 2010), and it was reduced during rest in Alzheimer's disease (Stam et al. 2005). Interestingly, LRTC are strongly attenuated in both of these disorders (Montez et al. 2009; Nikulin et al. 2012). Thus, it is plausible that multi-level criticality is important for long-distance neuronal communication and cognition, and the CROS model should prove valuable in determining this. To test this hypothesis, multiple CROS networks would need to be coupled to each other to understand how criticality of oscillations influences phase and amplitude correlations between networks. One way to compare with empirical data would require multiple resting-state recordings from the same subject. Neuronal networks would exhibit variability in criticality of oscillations, and phase-locking between different areas between these recordings. Therefore it could be determined if the criticality of the oscillations from these areas can explain differences in the level of phase-locking between them.

E/I and its future applications

Recording neuronal activity allows us to determine functions (Gray et al. 1989), and impairments in function (Leiser et al. 2011; Poil et al. 2013) of neuronal networks. In Chapter 4, I show that it is possible to estimate E/I of a neuronal network from its ongoing activity based on the network activity's closeness to the critical point. One way to further validate this method is by altering the E/I in human subjects, and seeing if $\widehat{E/I}$ detects it. This could be achieved through the use of pharmacology, with benzodiazepines being a thoroughly tested method to increase inhibition in a network which has been shown to have significant effects on neuronal oscillations recorded using MEG (Nutt et al. 2015). Another method to alter E/I is by applying transcranial direct current stimulation (Krause et al. 2013), which has also been shown to have significant effects on neuronal oscillations (Jacobson et al. 2012).

$\widehat{E/I}$ should enable high spatial-resolution estimation of E/I as it can be obtained from a single recording electrode. Methods of detecting neuronal criticality based on avalanche dynamics (Beggs and Plenz 2003; Petermann et al. 2009; Arviv et al. 2015) require multiple electrodes to detect the critical point which would lower the spatial resolution of the criticality estimate.

Fine-grained estimation of E/I would have important implications for detecting and treating imbalanced networks. It would allow for localized imbalances to be detected, and could allow for greater targeting of treatments. One likely candidate where this could prove helpful is in epilepsy patients where subjects are often treated with resection of areas showing imbalanced activity (Haegelen et al. 2013). Using recording electrodes which have finer spatial resolution it has been shown that epileptic events can be seen at multiple spatial scales, and that events at the smallest scales do not always lead to events at the largest scales (Stead et al. 2010). It will be interesting to see how localized $\widehat{E/I}$ is in the human cortex using different types of invasive recordings (Khodagholy et al. 2015) and whether any imbalances can also be detected during inter-ictal periods (Monto et al. 2007).

Critical oscillations and learning

One of the most important functions of a neuronal network is its ability to learn, likely through synaptic plasticity measures that alters the network structure (Martin et al. 2000). These measures have been shown to depend on the pre- and post-synaptic timing of spikes, and increase depending on repeated pairing (Caporale and Dan 2008). In chapter 2 we show that through LRTC the CROS model has meta-stable states that persist over multiple oscillation cycles, thus it is plausible that critical oscillations can set up meta-stable patterns that persist longer than the pairing and thus increase the memorability of the pattern stored in the network (Fiete et al. 2010). It is also plausible that once these patterns have been stored in the network, then spontaneous activity in the network will occasionally visit these states. Similar behavior has been seen in multi-cell spiking patterns in the rat hippocampus, where patterns of activity that were evoked when the animal was awake were replayed whilst the animal was asleep (Ji and Wilson 2007). It has been proposed that this replay of activity helps to consolidate memories learned during the day. In humans, memory consolidation during sleep has been shown to correlate with the strength of neuronal oscillations (Moroni et al. 2014). With LRTC of oscillations stretching to hundreds of seconds (Linkenkaer-Hansen et al. 2001), one function of LRTC could be to provide a support for storage and retrieval of memories.

Conclusion

Overall I show in this thesis that a greater knowledge of the mechanism and function of long-range temporal dynamics in neuronal networks will aid in understanding how the human cortex gives rise to perceptions, thoughts and behaviors.

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