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Feedback loops and oscillations in modular hierarchical brain networks: The topological origin of brain rhythms

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Introduction

Coupled systems often show oscillatory rhythms, for example, for predator-prey systems or the firing rate of neuronal populations. Whereas these oscillations have been studied for couplings of a few nodes, here we show how the topology of large-scale networks, leading to large feedback loops, influences oscillations. Oscillations or rhythms have been observed in brain networks, measured by the electroencephalogram (EEG). Starting from 1929, distinct frequency bands (e.g. alpha, beta, or gamma) were identified. These bands are the same for different species (Buzsaki, 2006). Similar frequency bands are also observed across different levels of neural organization—from EEG signals to local field potentials. Using the hierarchical modular organization of cortical networks (Kaiser et al., 2007), we find distinct frequency peaks of neural rhythms, with a ratio between peaks equivalent to the golden ratio φ (1.618...), Euler's number e , or multiples thereof. Our analysis replicates rhythms observed experimentally in various species, from rats to humans.

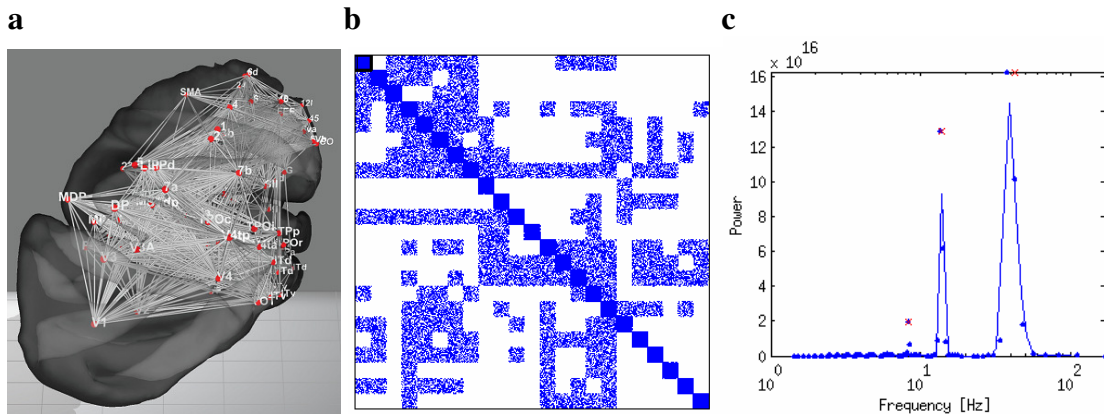


Figure 1. (a) Mammalian cortical fiber-tract network. (b) Hierarchical network of cortical regions with modular structure within regions (not shown). (c) Frequency peaks due to feedback loops in the network.

Results

We define the oscillation interval T that a signal propagates in a feedback loop as the path length of the loop L times the average delay of transmission D over a single connection. The oscillation frequency is thus $F=1/T=1/(L D)$. We used two delay values corresponding to slow or fast transmissions. We generated a hierarchical and modular neuronal network based on known cortical anatomy (Sporns et al., 2004). The network showed a hierarchical and self-similar structure of 23 regions, 25 columns within a region and 10 individual neurons within each column.

Each connection of the loop would add a small or large delay depending on whether a fast (90% probability) or slow (10% probability) axon was chosen. Peaks in the frequency power distribution arose both at the global and the local level (Fig. 1). In addition, many ratios between consecutive peaks are close to φ (1.618), φ^2 (2.618), and φ^3 (4.236) or multiples of e . All ratios are irrational, therefore leading to quasi-periodic patterns with minimum interference between different oscillation frequencies. The number of peaks depended on the delays and probabilities for fast and slow fibers. Using only a single delay, assuming only fast fibers, resulted in a single peak.

We have seen that the delay determines frequency peaks in our simulations. Therefore, longer fibers should influence delays and thus frequency peaks. In contrast, frequency bands in the small rat brain are the same as in the larger human brain. How can the delay stay comparable when the size of the brain increases by an order of magnitude, from about 10 mm in rats to more than 150 mm in humans? It is known that the probability that two neurons are connected decays almost exponentially with distance. Therefore, the increase of the average distance between neurons on the cortical surface does not lead to a corresponding increase in the number of long-distance connections: the average length of established axons for different brain sizes (rat, cat, macaque, human), assuming connection establishment decays with distance, remains comparable with 5.1 mm, 5.5 mm, 5.5 mm, and 5.5 mm, respectively.

Discussion

This study shows that hierarchical networks based on anatomical connectivity (Kaiser et al., 2007) can generate frequency distributions with (a) distinct frequency peaks, (b) peaks in similar ranges as known from electrophysiology, and (c) with ratios between peaks that are close to the irrational numbers φ or e which are beneficial for low signal interference (Roopun et al., under revision). Whereas in the present work we focused on the propagation of neural activity, the approach can be applied to other systems where nodes or edges introduce a delay for feedback loops, such as food webs or metabolic networks.

Acknowledgement

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