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Investigating the dynamic role of fluctuations in ongoing activity in the human brain

Dissertation submitted for the degree of Doctor of Philosophy of the University College London

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Declaration

I, Maren Urner, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

The work presented in Chapters 3 and 4 has been published as the following papers:

Urner, M., Schwarzkopf, D. S., Friston, K., Rees, G. (2013). Early visual learning induces long-lasting connectivity changes during rest in the human brain. Neuroimage 77, 148-56.

Urner, M. Sarri, M., Grahn, J., Manly, T., Rees, G., Friston, K. (2013). The role of prestimulus activity in visual extinction. Neuropsychologia 51(8), 1630-7.

"The fact that the body is lying down is no reason for supposing that the mind is at peace. Rest is… far from restful."
Seneca (~60 A.D. (1969))

Abstract

Traditionally, the focus in cognitive neuroscience has been on so-called evoked neural activity in response to certain stimuli or experiences. However, most of the brain's activity is actually spontaneous and therefore not ascribed to the processing of a certain task or stimulus – or in other words, uncoupled to overt stimuli or motor outputs. In this thesis I investigated the functional role of spontaneous activity with a focus on its role in contextual changes ranging from recent experiences of individuals to trial-by-trial variability in a certain task. I studied the nature of ongoing activity from two perspectives: One looking at *changes* in the ongoing activity due to learning, and the other one looking at the *predictive role* of prestimulus activity using different methodologies, i.e. EEG and fMRI. Finally, I ventured into the realm of inter-individual differences and mind-wandering to investigate the relationship between ongoing activity, certain behavioural traits and neuronal connectivity.

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Chapter 1 General introduction

1.1 Spontaneous and evoked activity

Traditionally, the focus in cognitive neuroscience has been on so-called evoked neural activity in response to certain stimuli or experiences. However, most of the brain's activity is actually spontaneous and therefore not ascribed to the processing of a certain task or stimulus – or in other words, uncoupled to overt stimuli or motor outputs. Possibly, the existence of ongoing intrinsic activity was first noted by Hans Berger when he introduced electroencephalography for humans in 1929 (Berger, 1929), asking whether "it [is] possible to demonstrate the influence of intellectual work upon the human electroencephalogram, insofar as it has been reported here?" to conclude subsequently that "[o]f course, one should not at first entertain too high hopes with regard to this, because mental work, as I explained elsewhere, adds only a small increment to the cortical work which is going on continuously and not only in the waking state". Four years later, Bishop (1933) reported the potential physiological significance of the ongoing activity describing his experiments with rabbits. He observed cyclic changes in the excitability in visual cortex during stimulation of the optic nerve. Summarising his findings, he stated that "[…] we would look upon the cortex as being in constant activity, the physiological activity of the whole network of neurons bearing some direct relationship to the 'present state' of the animal's complex behavio[u]r which is sometimes referred to as his 'mental state'".

Indeed, ongoing activity occurs throughout the brain and its existence is manifested in the variability of cortical responses in repeated responses to physically identical

conditions or stimuli. In the past, this variability had simply been labelled as noise and scientists got rid of it by averaging over repeated trials (Gerstein, 1960; Zohary et al., 1994). However, during the last two decades an increasing number of neuroscientists recognised that ongoing neural activity is not mere noise, but plays a fundamental role in stimulus-driven processing (Arieli et al., 1996; Tsodyks et al., 1999) and behavioural variability indeed (Hesselmann, Kell, Eger, et al., 2008; Coste et al., 2011; Kleinschmidt et al., 2012).

I investigated the characteristics of the ongoing brain activity[1] focusing on its functional role and its role in contextual changes, where contextual changes can be differences in the experience of individuals (e.g. learning-related changes) or can be related to trial-by-trial variability.

1.2 The study of spontaneous activity

Why study ongoing brain activity? Contrary to the focus on evoked activity in neuroscience, spontaneous neural activity dominates the brain's energy consumption (Attwell and Laughlin, 2001; Mintun et al., 2001; Attwell and Iadecola, 2002). The energy consumption during rest exceeds task-related increases in neural metabolism, which are usually < 5 % (Raichle and Mintun, 2006). Thus, the majority of neuroscientific studies are focused on a minor component of brain activity. Maybe it is time for an adjustment or alteration in the neurosciences, shifting towards an

[1] In the literature, different terms have been used to describe ongoing neural activity – as compared to evoked responses – among which are "resting state activity", "endogenous activity", "spontaneous activity", and "autonomous activity". I use the term "ongoing activity" and "spontaneous fluctuations" interchangeably and refer to activity not evoked by an external stimulus or task.

experimental approach that is indeed focusing on the factor that uses the lion's share of the brain's energy, namely ongoing or spontaneous neural activity.

Although ongoing brain activity has been studied using electrophysiological and neuroimaging methods, its physiological origin and cognitive consequences are not yet fully understood. Crucially, any clarification is difficult by its very nature, because any study that addresses the functional significance of spontaneous fluctuations inevitably requires a primary task-context in order to probe perceptual and / or behavioural consequences of the fluctuations (Hesselmann, Kell, and Kleinschmidt, 2008). Attributed roles of ongoing brain activity span processes at different levels of neural activity and range from the traditional view of "intrinsic noise" over low-level physiological processes and uncontrolled mental activity to a monitoring of the environment (Mantini and Vanduffel, 2013). In conclusion, one of the most intriguing questions in the neurosciences might be related to the functional significance of the brain's "intrinsic noise".

1.2.1 Electrophysiological research of ongoing activity

The brain is a noisy system whose processing parts – the neurons – receive a large number of fluctuating inputs which in turn generate spike patterns. These often appear very irregular and much of the activity is spontaneous.

1.2.1.1 Cortical states and response variability

Cortical states are determined by the states of individual neurons and the states of individual neurons are in turn related to the state of their neighbours. Possibly the ground-breaking study investigating spontaneous activity and its relation to the large variability of evoked responses to repeated presentations of the same stimulus, is the