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Surface EEG shows that functional segregation via phase coupling contributes to the neural substrate of mental calculations

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ABSTRACT

Multichannel EEG traces from healthy subjects are used to investigate the brain's self-organisation tendencies during two different mental arithmetic tasks. By making a comparison with a control-state in the form of a classification problem, we can detect and quantify the changes in coordinated brain activity in terms of functional connectivity. The interactions are quantified at the level of EEG sensors through descriptors that differ over the nature of functional dependencies sought (linear vs. nonlinear) and over the specific form of the measures employed (amplitude/phase covariation). Functional connectivity graphs (FCGs) are analysed with a novel clustering algorithm, and the resulting segregations enter an appropriate discriminant function.

The magnitude of the contrast function depends on the frequency-band (θ, α_1, α_2, β and γ) and the neural synchrony descriptor. We first show that the maximal-contrast corresponds to a phase coupling descriptor and then identify the corresponding spatial patterns that represent best the task-induced changes for each frequency band.

The principal finding of this study is that, during mental calculations, phase synchrony plays a crucial role in the segregation into distinct functional domains, and this segregation is the most prominent feature of the brain's self-organisation as this is reflected in sensor space.

1. Introduction

The brain's remarkable ability to self-organise, not only in response to sensory stimulation but also as a result of endogenous information processing, has repeatedly been demonstrated in the past. Modern neuroimaging techniques facilitate the observation of pattern formation in intact brain and at multiple time and space scales. Recent methodological innovations have opened the possibility of studying and tracking emerging patterns that are based on various signals and derived representations (Mitra & Bokil, 2007). In this way, various cognitive tasks have been decomposed into different sub-processes, with the underlying neural mechanisms characterised in sufficient detail. The prevailing notion of a dynamical complex system, whose behaviour is governed via abrupt phase transitions, has led to the systematisation of coordination principles (Kelso, 1995). The interplay of functional segregation into local brain areas and global integration through distant interactions is considered the hallmark of self-organisation (Srinivasan, Russell, Edelman, & Tononi, 1999).

Mathematical thinking as a cognitive process activates not only local but also spatially distributed cortical networks, depending upon task specificity and complexity (Micheloyannis, Sakkalis, Vourkas, Stam, & Simos, 2005). Mathematical thinking is also strongly correlated with working memory capacity, language function and general intelligence. Simpler arithmetic tasks, such as simple addition, simple subtraction and multiplication, are correlated with language and long-term explicit semantic memory (Dehaene, Molko, Cohen, & Wilson, 2004). Comparisons between quantities primarily activate the bilateral intraparietal sulcus (Delazer et al., 2003; Barth et al., 2006). Frontal and parietal regions are the most common regions to be reported in the literature to be related to mathematical thinking (Barnea-Goraly, Eliez, Menon, Bammer, & Reiss, 2005; Dehaene, Piazza, Pinel, & Cohen, 2003; Rivera, Reiss, Eckert, & Menon, 2005). In addition, an asymmetry between the left and right hemispheres, with a predominance of the left hemisphere in simple arithmetic calculations, has been reported (Rivera et al., 2005; Zhang, Zhang, Zhang, & Li,

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2005). Two-digit multiplications are rather difficult calculations that demand retrieval of simple mathematical facts and, in addition, require adherence to a series of mental calculation procedures that exemplify higher order mathematical thinking (Gruber, Keil, & Muller, 2001). These processes are expected to engage a network of areas that are responsible, among others, for language functions, including long-term (consolidated) and verbal memory (Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999; Delazer et al., 2003) as well as verbal working memory (Micheloyannis et al., 2009).

Functional MRI (fMRI) has been used to precisely localise the non-verbal quantity representation system. The results indicate that numerical tasks typically involve a distributed network, including frontal cortex areas and left/right parietal lobes (Chochon, Cohen, Van De Moortele, & Dehaene, 1999; Dehaene et al., 1999; Pesenti, Thioux, Seron, & De Volder, 2000; Piazza, Giacomini, Le Bihan, & Dehaene, 2003; Pinel, Dehaene, Riviere, & Lebihan, 2001; Pinel, Piazza, Le Bihan, & Dehaene, 2004; Rickard et al., 2000). Hemodynamic brain imaging techniques, however, lack the temporal resolution necessary to reveal rapidly changing patterns of local neurophysiological responses and functional connections between brain areas that are part of the brain mechanism that support the performance of a specific cognitive task. Aiming at finer temporal scales, EEG studies have started to appear. Changes in local and coordinated activity were investigated using linear and non-linear measures of the EEG signal in different arithmetic tasks (Micheloyannis et al., 2005). The results indicated that the pattern of neural synchrony varies with the complexity of the performed task, depending on the frequency band, and corresponds to a distributed set of neural networks. Event related potential (ERP) paradigms have also been adapted for the exploration of brain activity during mental arithmetics (Duhong, Jian, & Hongtao, 2011; Wang et al., 2007).

Having in mind to study math-related cognition as a brain state manifestation, we adopted an experimental design that deviates from the traditional approach in which a particular simple arithmetic operation is targeted at. We incorporated more demanding tasks, namely the multiplication of two-digits numbers and the four-digits comparison, instead. These two mathematical tasks depend upon neurophysiological processes that are known to differ regarding their nature and the distribution of the activated brain regions. According to several neuroimaging studies, comparison is a more localised procedure (activating intraparietal brain region) while difficult (two-digits) multiplication demands the activation of a widely distributed network (Micheloyannis et al., 2005 ; Dehaene, 1996; Pinel et al., 2001). The initial motivation was to describe the functional (re)organisation, during the execution of these two tasks, by detecting neural networks according to a graph theoretic perspective (Bullmore & Bassett, 2011).

The principal scope of this study was to investigate whether the emergence of functional clusters is an important mode of pattern formation underlying the cognitive load of two mental calculation tasks and whether these clusters have sufficient signal deviation from the baseline condition. Specifically, we considered the multichannel EEG recordings during rest and active conditions (subjects performing either difficult multiplication or number comparisons) as observations from two different states of the (same) brain, which could be discriminated by a common classification algorithm, and searched for a specific state-representation that would facilitate the best discrimination. Discriminability was measured for different types of coupling (linear vs. nonlinear) and different forms of covariation (amplitude/phase). Because discrimination was formulated independently of a given state representation, it could be expressed in a common scale and accompanied by its statistical significance (calculated using the distribution of random state-assignments). The resting-state vs. active-state classifications with the most prominent separation were identified independently for each frequency-band, and prototypical topographies (representative segregations) best describing each state were extracted and characterised.

This comparative study appointed phase-synchrony as the most important aspect of cognitive processes that underlie mental calculations and showed that segregation into distinct functional networks was an important dimension of task-induced changes. It must, however, be stressed that these interrelationships refer to nodes representing EEG sensor signals that may only approximately relate to actual neural generators.

This paper is organised as follows. In Section 2, after a short description of the experimental data, we describe our procedure for validating class-separability, and we briefly describe the ways to test task-induced differences. Section 3 is devoted to the results from the comparative study of neural synchrony. Section 4 discusses the importance of our findings and their correlation with recent relevant literature, and Section 5 includes the conclusions.

2. Methods

2.1. The experimental data

2.1.1. Subjects

The present study concerned 18 right-handed volunteers (aged: 21–26 years, mean 23 years, who were Medical School students in the University of Crete) during the performance of arithmetic tasks differing in the nature and level of complexity. All of the participants signed an informed consent form after the procedures were explained to them, had normal or corrected-to-normal vision and reported no history of verbal or non-verbal learning disability (all medical students in Greece go through a rigorous national testing process that includes advanced math and written composition).

2.1.2. EEG recordings

EEG was recorded continuously while subjects were performing one of the two arithmetic tasks: (1) four-digit number comparisons (e.g., 5467 vs. 6689; numbers in "different pairs" differed by less than 20%) in which the position of the larger number varied randomly, and participants had to raise their left index finger if the number on top was greater and had to raise their right left index finger otherwise; (2) two-digit multiplication (e.g., 34×23, 49×32), in which participants were allowed 10 s from the time the number stimuli were presented on the screen until either a fixation spot was presented (in the number comparison task) or a number was briefly flashed on the screen (in the multiplication task), and they had to respond as to whether the number coincided with the correct result or not. An additional EEG baseline was recorded during a passive viewing condition (i.e., participants simply fixated at the centre of the computer screen on a small star). Stimuli were presented on an LCD screen located in front of the participants at a distance of approximately 80 cm, subtending 2–3° and 2–4° of the horizontal and vertical visual angle, respectively. Each stimulus was always present for 1.5 s, while a fixation star was presented during the ISI for a 0.5 s duration. The three tasks (control, multiplication and comparisons) were delivered in trials of random order to the subject, who then had 10 s to execute each task using the numbers presented on the screen (or simply to rest in the case of the first task). During the comparison task we were presenting, successively, different pairs of 4-digits numbers, since each single comparison was accomplished in a short time. The subject indicated its response via finger rising, which was recorded via an optical switch, and the visual stimulus was switched to the new comparison. Fig. 1 provides a schematic description of the experimental flow. An experienced neurophysiologist (SM) was inspecting the signals on the monitor of the recording PC and decided