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EFFORTFUL CONTROL AND RESTING STATE NETWORKS: A LONGITUDINAL EEG STUDY

GENNADY G. KNYAZEV, [a]* ALEXANDER N. SAVOSTYANOV, [a,b] ANDREY V. BOCHAROV, [a,b] HELENA R. SLOBODSKAYA, [a,b] NADEZHDA B. BAIROVA, [a] SERGEY S. TAMOZHNIKOV [a] AND VALENTINA V. STEPANOVA [c]

[a] *Institute of Physiology and Basic Medicine, Novosibirsk, Russia*

[b] *Novosibirsk StateUniversity, Novosibirsk, Russia*

[c] *Limited (Liability) Company, "Harmony", Smolensk, Russia*

Abstract—Resting state networks' (RSNs) architecture is well delineated in mature brain, but our understanding of their development remains limited. Particularly, there are few longitudinal studies. Besides, all existing evidence is obtained using functional magnetic resonance imaging (fMRI) and there are no data on electrophysiological correlates of RSN maturation. We acquired three yearly waves of resting state EEG data in 80 children between 7 and 9 years and in 55 adults. Children's parents filled in the Effortful Control (EC) scale. Seed-based oscillatory power envelope correlation in conjunction with beamformer spatial filtering was used to obtain electrophysiological signatures of the default mode network (DMN) and two task-positive networks (TPN). In line with existing fMRI evidence, both cross-sectional comparison with adults and longitudinal analysis showed that the general pattern of maturation consisted in an increase in long-distance connections with posterior cortical regions and a decrease in short connections within prefrontal cortical areas. Latent growth curve analysis showed that EC scores were predicted by a linear increase over time in DMN integrity in alpha band and an increase in the segregation between DMN and TPN in beta band. These data confirm the neural basis of observed in fMRI research maturation-related changes and show that integrity of the DMN and sufficient level of segregation between DMN and TPN is a prerequisite for appropriate attentional and behavioral control.

Key words: EEG, resting-state networks, functional connectivity, children, longitudinal study, effortful control.

INTRODUCTION

The discovery of the so-called resting state (RSNs) or intrinsic connectivity networks is perhaps the most significant breakthrough in human neuroscience in the current century. This discovery has been done using functional magnetic resonance imaging (fMRI, Biswal et al., 1995), which showed that brain activity in spatially separate, but functionally related regions exhibit temporal correlation even in the absence of a task. Later studies showed that similar correlation structure could be recovered from fMRI data obtained in different kinds of tasks and that a handful of RSNs are highly functionally relevant (Smith et al., 2009). Some RSNs are associated with sensory processing (such as visual and auditory networks); others support attention and cognition (such as attentional and default mode networks). The default mode network (DMN), which includes the precuneus/posterior cingulate cortex (PCC), the medial prefrontal cortex (MPFC), and medial, lateral, and inferior parietal cortex, has particularly attracted attention of researchers, because it is the only network, which is more active during rest than during the performance of a task (Raichle et al., 2001). Some authors propose that the DMN supports 'self-referential' or 'introspective' mental activity (Gusnard et al., 2001). However, some authors believe that it may have a much more fundamental role in brain function, playing a critical role in the organization of preplanned, reflexive behaviors that are critical to our existence (Raichle, 2015). Recent reports suggest DMN functions are related to executive behavior (Gilbert et al., 2006, 2007; Weissman et al., 2006) and reward processing (Luhmann et al., 2008). The balance between the DMN and the networks controlling spatial attention and executive control appears to be critical in determining the output of motor planning and, ultimately, the subject's level of impulsivity (Shannon et al., 2011).

Contrary to DMN, which is frequently called 'task-negative network', several networks show a consistent pattern of activation in attention demanding tasks and are correspondingly called 'task-positive networks'

*Corresponding author. Address: Institute of Physiology and Basic Medicine, Timakova str, 4, Novosibirsk 630117, Russia. Fax: +7-383-335-97-54.

E-mail address: knyazev@physiol.ru (G. G. Knyazev).

Abbreviations: ACC, anterior cingulate cortex; AIns, anterior insula; ANOVA, analysis of variance; BEM, boundary element model; BOLD, blood oxygen level dependent; CEN, central executive network; DlPFC, dorsolateral prefrontal cortex; DMN, default mode network; EC, effortful control; EEG, electroencephalography; FDR, false discovery rate; FEW, family wise error; fMRI, functional magnetic resonance imaging; GOF, goodness-of-fit; IAF, individual alpha peak frequency; LCMV, linearly constrained minimum variance; LGM, latent growth curve; LME, linear mixed effects; MEG, magnetoencephalography; MNI, Montreal neurological institute; MPFC, medial prefrontal cortex; PCC, posterior cingulate cortex; PET, positron emission tomography; PFC, prefrontal cortex; RFT, random field theory; ROI, region of interest; RSN, resting state network; SAL, salience network; SNR, signal to noise ratio; SwE, Sandwich Estimator.

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(TPN). Two task-positive networks are particularly important for behavioral control – the central executive (CEN) and the salience (SAL) networks (Seeley et al., 2007). The CEN (also called the fronto-parietal control network; Vincent et al., 2008) is anchored in the dorsolateral prefrontal cortex (DlPFC) and posterior parietal cortex, whereas the SAL (also called the cinguloopercular network; Dosenbach et al., 2007) has main hubs in the dorsal anterior cingulate and orbitofrontal insular cortices. Activity in the CEN correlates positively with performance on executive control tasks (Seeley et al., 2007); the strength of within-network connectivity is associated with IQ in children (Langeslag et al., 2013). The SAL, on the other hand, may implement stable task control across the trials of a task (Dosenbach et al., 2007).

A very important issue is the concept of a functional balance between the DMN and the TPN (Raichle, 2015). It appears that these networks are not only functionally anticorrelated (i.e., DMN is active when TPN is idle and vice versa), but show anticorrelations in the resting state (Fox et al., 2005). While the data-processing procedures that revealed this relationship (i.e., regressing out the whole-brain signal averaged over all voxels) has been criticized by some authors, as it may artificially introduce anticorrelations into fMRI data (Murphy et al., 2009), others argued that this procedure enhances the detection of system-specific correlations and improves the correspondence between resting-state correlations and anatomy (Fox et al., 2009). Later studies showed that anticorrelation between DMN and TPN could be demonstrated without global signal regression (Allen et al., 2012; Chai et al., 2012). Moreover, reciprocal relationship between DMN and TPN appears to be highly functionally relevant, because it changes in psychopathological conditions (Chai et al., 2011; Hamilton et al., 2011; Marchetti et al., 2012; Knyazev et al., 2016) and across development (Barber et al., 2013).

RSN structure and function has been predominantly investigated using fMRI. However, the fMRI blood-oxygen-level-dependent (BOLD) signal only indirectly relates to neuronal events (Debener et al., 2006). Therefore, a replication of fMRI findings in electrophysiological domain is vitally important. A number of magnetoencephalographic (MEG) and electroencephalographic (EEG) studies have investigated RSNs (see O'Neill et al., 2015 for a review). Using seed-based oscillatory power envelope correlation or independent component analysis in conjunction with beamformer or Minimum Norm Estimation source localization techniques, these studies have revealed RSNs similar in their spatial organization to ones described in fMRI research in both MEG (de Pasquale et al., 2010; Brookes et al., 2011a,b, 2012a,b; Hall et al., 2013, 2014; Hipp et al., 2012; Hipp and Siegel, 2015; Liu et al., 2010; Luckhoo et al., 2012; Wens et al., 2014a,b) and EEG (Knyazev et al., 2016; Siems et al., 2016) data. These findings are encouraging because they imply that RSNs may have electrophysiological underpinning and are directly related to coordinated neuronal activity in the brain. Moreover, these findings link RSNs with specific EEG frequency bands, whose functional correlates are relatively well known, and pave the way for the study of RSNs dynamics on ms temporal scales, which is not accessible for fMRI in principle. In resting state MEG and EEG data, DMN spatial organization has been most reliably reproduced in alpha and beta frequency bands (de Pasquale and Marzetti, 2014; Brookes et al., 2011b; Knyazev et al., 2011, 2016; Wens et al., 2014b). Alpha and beta oscillations also most frequently emerge as a correlate of DMN activity in simultaneous EEG-fMRI studies (Ben-Simon et al., 2008; Hlinka et al., 2010; Jann et al., 2009, 2010; Mantini et al., 2007; Wu et al., 2010) and in studies investigating presumable functional correlates of DMN activity (Knyazev, 2013; Marzetti et al., 2014). The association between alpha/beta and task-positive networks has also been repeatedly noted (Brookes et al., 2012a; Ben-Simon et al., 2008; Chen et al., 2012; Luckhoo et al., 2012; Sadaghiani et al., 2010, 2012).

While the architecture of functional networks is relatively well delineated in the mature adult brain, our understanding of its development remains limited. A number of cross-sectional studies compared connectivity within and between networks in adults and children of different ages. These studies suggest earlier maturation of primary functional networks, such as the visual and the auditory networks (Fransson et al., 2007), than higher order ones, which experience prolonged postnatal development (Fair et al., 2008; Supekar et al., 2009). Moreover, increasing integration within each functional network and segregation between this and other networks occurs throughout childhood and adolescence (Vogel et al., 2010). Using support vector machine-based multivariate pattern analysis, Dosenbach et al. (2010) show that fMRI connectivity measures could accurately predict individuals' brain maturity across development from 7 to 30 years. The weakening of short-range functional connections made the greatest relative contribution to the prediction.

The DMN have been identified very early in development, i.e., in 2-week-old to 2-year-old healthy pediatric subjects (Gao et al., 2009). However, as compared to adults, infants exhibit weaker connectivity in the PCC node of the DMN, but higher connectivity in MPFC/anterior cingulate cortex (ACC) (Wylie et al., 2014). Even at early school age, the default regions are only sparsely connected (Fair et al., 2007; de Bie et al., 2012; Muetzel et al., 2016). A combination of structural and functional connectivity analyses suggested that PCC-MPFC connectivity along the cingulum bundle is the most immature link in the DMN of 7- to 9-year-old children (Supekar et al., 2009). Washington and VanMeter (2015) also show that connectivity between ACC/MPFC and PCC DMN nodes significantly increased as a quadratic function of age in a sample of 6- to 25-year olds. An increase in the antero-posterior DMN connectivity with age has been shown in large samples of Brazilian (Sato et al., 2014) and Spanish (Solé-Padullés et al., 2016) children. No effect of sex, nor age by sex interactions was observed in the latter study. Increased functional segregation (decreased short-range connections) and integration (increased long-range connections) and an increase in the antero-posterior connectivity during childhood were