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Delta-gamma coupling as a potential neurophysiological mechanism of fluid intelligence

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ABSTRACT

Electrophysiological investigations have pointed out significant yet weak correlations between intelligence and oscillatory brain activity, including the spectral power, frequency, complexity, synchrony, and coherence of electroencephalographic (EEG) signals, however neglecting the interplay between fast and slow neuronal oscillations underlying information transfer in the brain. We found that fluid intelligence level (*gf*) depends on the precise synchronization of fast oscillations to a specific time window of slow brain rhythms. Specifically, by examining EEG recordings of 50 people in resting state as well as during performance at two *gf* tasks we found converging evidence that high-*gf* participants display stronger Phase-Amplitude Coupling (PAC) related to an increased concentration of gamma (~36 Hz) spectral power at the descending phase of delta oscillations (~3 Hz). Delta-gamma PAC strength explained 35% variance in scores on multiple *gf* tests, outperforming six alternative EEG-based predictors including spectral power, complexity and amplitude-amplitude coupling. Present results suggest PAC as a neurophysiological substrate of *gf* in humans, offering novel insight about the role of slow and fast brain rhytms in high-order cognition, as well as a potential new target for neuromodulatory interventions in the healthy and pathological brain.

1. Introduction

Academic and professional success, socio-economic status, and even longevity are all strongly predicted by individual level of psychometric intelligence (Deary, 2012). A key component of intelligence is called fluid intelligence (*gf*), and is assessed as the ability to solve novel problems via abstract reasoning, regardless of prior knowledge and domain-specific skills (McGrew, 2009). Because performance in multiple cognitive domains, including linguistic and mathematical abilities, learning, self-control, and even social skills are strongly correlated with *gf*, decades of research were devoted to understanding the neuronal mechanisms underlying inter-individual differences in *gf* (Colom, Karama, Jung, & Haier, 2010; Deary, Penke, & Johnson, 2010). Multiple neurobiological factors that predict *gf* were found, including structural properties of the neocortex (e.g., Barbey, Colom, Paul, & Grafman, 2014; Basten, Hilger, & Fiebach, 2015; Colom et al., 2009, 2013), integrity of subcortical fiber tracts (e.g., Clayden et al., 2012; Jung & Haier, 2007; Othani et al., 2014; Pineda-Pardo, Martinez, Roman, & Colom, 2016), brain efficiency (e.g., van den Heuvel, Stam, Kahn, & Pol, 2009; Pineda-Pardo et al., 2016), metabolic levels in fronto-parietal regions (e.g., Basten et al., 2015; Dunst et al., 2014; Neubauer & Fink, 2009; Santarnecchi et al., 2017), and organization of spontaneous functional brain activity (e.g., Cole, Yarkoni, Repovs, Anticevic, & Braver, 2012; Finn et al., 2015; Santarnecchi et al., 2015; Schultz & Cole, 2016).

However, each factor explain no more than 25% of interindividual variance in *gf*, and it is not clear how most of those neurobiological factors actually contribute to more effective cognitive performance of high-*gf* individuals. For example, no theory actually provides a quantitative explanation of why and how, for instance, more gray matter in the neocortex and higher integrity of white matter tracts should translate into more valid abstract reasoning in complex cognitive tasks,

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even though intuitive explanations might be drawn. Also, the relationship between metabolic efficiency during a cognitive task and intelligence is complex, adaptive (Dunst et al., 2014), and whether intelligent brains display lower or higher metabolism depends on many moderators, e.g. the task itself, its relative difficulty, instruction, sex and expertise (Neubauer & Fink, 2009). Finally, brain connectivity studies diverge on whether intelligence is related to either single, local hubs (Cole et al., 2012) or to distributed, global properties (Santarnecchi et al., 2015; van den Heuvel et al., 2009).

By contrast, information-processing theories explain abstract reasoning in terms of effective maintenance, control, and transformation of task-relevant mental structures in the working memory system (e.g., Carpenter, Just, & Shell, 1990; Johnson-Laird, 2006; Ragni & Knauff, 2013). Information within this system is highly accessible, but its duration and capacity are limited (Cowan, 2001). Numerous studies suggest that working memory capacity explains at least 50% of variance in *gf* (e.g., Chuderski, 2013; Kane, Hambrick, & Conway, 2005), being its strongest predictor thus far. However, working memory is a construct not so much simpler than *gf* itself, thus it is not easy to link its capacity to neurophysiology of the human brain. A growing number of primate studies (e.g., Naya & Suzuki, 2011; Siegel, Warden, & Miller, 2009) are showing how information encoding during working memory performance may be underpinned by patterns of both synchronous and asynchronous neuronal oscillations. The role of oscillatory patterns for working memory capacity has been also suggested by intracranial recordings from epileptic patients (e.g., Axmacher et al., 2010; Leszczynski, Fell, & Axmacher, 2015; van Vugt, Schulze-Bonhage, Litt, Brandt, & Kahana, 2010). Such oscillations are also key mechanism in leading neurocomputational models of working memory (e.g., Horn & Usher, 1991; Lisman & Idiart, 1995; Vogel, Woodman, & Luck, 2001) and reasoning (e.g., Eliasmith et al., 2012; Knowlton, Morrison, Hummel, & Holyoak, 2012), which thus link cognitive performance with the interplay between brain oscillatory patterns. In line with this research, our own model (Chuderski & Andrelczyk, 2015) assumed that cross-frequency coupling (CFC) between slow and fast brain oscillations underlying storage and control of information in working memory might play a pivotal role in individual differences in abstract reasoning, and thus might strongly predict *gf*. The goal of the present study was to examine this prediction using electroencephalography (EEG) data collected during *gf* problem-solving in healthy participants.

CFC is considered the optimal coding scheme supporting local and distant information transfer in the human brain (Canolty et al., 2006; Jensen & Colgin, 2007). Specifically, the phase-amplitude modulation of high-frequency electrical activity in the beta (2^4–2^5 Hz) or gamma bands (2^5–2^8 Hz) by the phase of low-frequency delta (2^1–2^2 Hz), theta (2^2–2^3 Hz), or alpha rhythms (2^3–2^4 Hz), observed in electrocorticographic (ECoG) as well as electroencephalographic (EEG) data, has been shown to underpin performance in multiple perceptual, attentional, and memory tasks (Canolty & Knight, 2010; Lisman & Jensen, 2013). For instance, stronger theta/delta modulation of gamma band activity in a spatial cuing task improves focused attention (Szczepanski et al., 2014), while bursts of gamma activity at different phase of the delta cycle seems to reflect mental representation of different categories of objects (faces, scenes, houses, or tools; Watrous, Deuker, Fell, & Axmacher, 2015).

Although several ECoG (e.g., Axmacher et al., 2010; Leszczynski et al., 2015) and EEG studies (e.g., Sauseng et al., 2009) indicated that working capacity may depend on the interplay between amplitude of gamma activity and the phase of theta/alpha, and an EEG study has suggested a weak negative link between resting-state theta-gamma amplitude-amplitude coupling (AAC) and intelligence (Pahor & Jaušovec, 2014b), no study to date has investigated the role of PAC during *gf*-related problem-solving. The present study aimed at the comprehensive investigation of relationships between PAC present in EEG data and *gf*, the latter assessed by the scores on multiple abstract reasoning tests. Specifically, our goal was to identify specific frequencies (if any) involved in PAC, which would most strongly contribute to *gf*. As to date several other EEG-based neurophysiological markers were associated with intelligence, we also aimed to compare the potential contribution of PAC to *gf* to the contribution of these alternative markers.

2. Materials and methods

2.1. Participants

We recruited 33 women and 24 men via internet adverts. For one three-hour session, participants were paid the equivalent of 10 euro in local currency. Mean age was 22.3 years (SD = 2.8, range 19–35). Participants were screened for normal or corrected-to-normal vision and no history of neurological problems, and informed that they could interrupt the data collection and exit the study at any moment. They signed a written consent to participate. Each participant was tested in soundproof, dimly-lit cabin, under the supervision of an experimenter. The study conformed to ethical guidelines of National Science Center of Poland: http://www.ncn.gov.pl/sites/default/files/pliki/2016_zalecenia_Rady_NCN_dot_etyki_badan.pdf, as well as fully conformed to Declaration of Helsinki. Because of either low quality of electroencephalographic (EEG) signal or procedural errors during signal recording, the data from 7 participants had to be discarded from analysis, leading to a final sample of 50 people.

2.2. EEG procedure

First, continuous resting EEG was recorded for 180 s with eyes open and 180 s with eyes closed (Fig. 1). Only eyes closed data was submitted to analysis (henceforth called *Rest* condition). Next, participants performed a computerized variant of Raven's Advanced Progressive

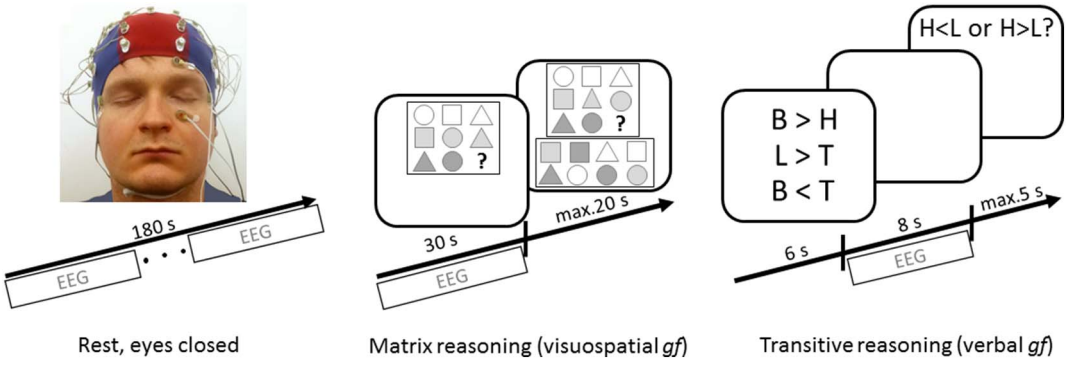

Fig. 1. Experimental design. EEG was recorded both during resting-state and during the solution of two tasks assessing visuospatial and verbal *gf* performance. For additional information see the method section of the paper.

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