



Theta–gamma cross-frequency coupling relates to the level of human intelligence

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ABSTRACT

In order to examine whether theta–gamma cross-frequency relates to intelligence, two EEG experiments were conducted on healthy participants. In the first experiment, theta–gamma functional coupling was determined based on resting (eyes closed) EEG data of 100 participants. Twenty participants with either low or high theta–gamma correlation coefficients were asked to participate in the second experiment in which they were presented with a test of fluid intelligence. The results showed that: (1) resting-state theta–gamma cross-frequency coupling in bilateral frontal and parieto-occipital areas negatively correlated with IQ scores and (2) theta–gamma cross-frequency coupling in frontal areas correlated with performance on the test of fluid intelligence. Individuals with low theta–gamma coupling during rest showed an increase in theta–gamma functional coupling in frontal areas as task difficulty increased, which was associated with better performance on the test. These findings demonstrate for the first time that theta–gamma cross-frequency coupling in frontal areas, and partly also in parietal areas (Experiment 1), relates to the level of intelligence.

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1. Introduction

There is converging evidence that cross-frequency coupling between theta and gamma oscillations plays an important role in working memory processing (for a review see Roux & Uhlhaas, 2014; Canolty & Knight, 2010; Jensen & Colgin, 2007). Research from rodent studies suggests that in the hippocampus, gamma frequency oscillations are nested within theta oscillations, which enables the representation of multi-item messages that are relevant for working and long-term memory (Belluscio, Mizuseki, Schmidt, Kempter, & Buzsáki, 2012; Bragin et al., 1995; Colgin et al., 2009; Fuchs et al., 2007; Lisman & Jensen, 2013; Senior, Huxter, Allen, O'Neill, & Csicsvari, 2008). Similar findings have been demonstrated in human studies. Axmacher et al. (2010) showed that maintenance of multiple items is associated with hippocampal theta–

gamma cross-frequency coupling and that the modulating theta frequency depends on memory load. Theta–gamma phase synchronization during performance on visual working memory tasks has also been reported for healthy subjects (Holz, Glennon, Prendergast, & Sauseng, 2010; Schack, Vath, Petsche, Geissler, & Möller, 2002). Further, Kamiński, Brzezicka, and Wróbel (2011) demonstrated that short term memory capacity can be predicted by theta-to-gamma cycle length ratio. Long-term memory has also been associated with cross-frequency coupling between theta band activity in frontal brain areas and gamma band activity in parietal and occipital areas (Frieze et al., 2013). Moreover, theta and gamma oscillations during encoding predict subsequent memory recall (Sederberg, Kahana, Howard, Donner, & Madsen, 2003) and retrieval (Osipova et al., 2006). Several studies have shown that theta synchronizes during working memory processes and acts as a gating mechanism, providing optimal neural conditions for specific processing (Klimesch, Freunberger, Sauseng, & Gruber, 2008; Klimesch, Vogt, & Doppelmayr, 1999; Raghavachari et al., 2001; Sauseng, Griesmayr, Freunberger, & Klimesch, 2010).

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Psychometric research has revealed a positive relationship between performance on tasks of working memory and fluid intelligence, with correlations ranking from 0.60 to 0.90 (Burgess, Gray, Conway, & Braver, 2011; for a review see Buehner, Krumm, & Pick, 2005). It has also been demonstrated that working memory capacity largely accounts for the relationship between working memory and intelligence, and that processing components like updating and control of attention (related to frontal brain processing) have a negligible or non-existent relationship with intelligence (e.g. Colom, Abad, Quiroga, Chun, & Flores-Mendoza, 2008; for a review see Ackerman, Beier, & Boyle, 2005).

Hence, one could assume that there is also a relationship between intelligence and theta–gamma cross-frequency coupling. In order to examine if such a relationship exists, an EEG study was conducted in which (1) resting eyes-closed cross-frequency theta–gamma coupling was correlated with performance on IQ tests; and (2) the relationship between theta–gamma cross-frequency coupling during performance on easy and difficult Raven's progressive matrices (RAPM; Raven, 1990) was investigated. Given that, to our knowledge, this is the first study to investigate the relationship between intelligence and theta–gamma cross-frequency coupling, the nature of the study was exploratory.

2. Experiment 1

In the first experiment we examined the relationship between the level of intelligence and theta–gamma cross-frequency coupling.

2.1. Method

2.1.1. Participants

One hundred right-handed students (mean age 20 years and 2 months; 50 of them female) were selected from a large pool of participants ($N = 417$) that had been tested with the Wechsler Adult Intelligence Scale test battery (WAIS; Wechsler, 1981). The participants' IQ scores resembled a normal distribution of intelligence both in the whole sample and in the male and female subsamples (see Table 1). The experiment was undertaken with the understanding and written consent of each subject, following the recommendations of the ethics committee of the Slovene Psychological Association.

2.1.2. Procedure and EEG recording

The subjects were told that they would be participating in an EEG study. They were asked to completely relax in a reclining chair with eyes closed while their resting EEG was recorded for a period of 3 min. EEG was recorded using a Quick-

Cap with sintered (silver/silver chloride; 8 mm diameter) electrodes. Using the Ten–Twenty Electrode Placement System of the International Federation, EEG activity was monitored over nineteen scalp locations (Fp1, Fp2, F3, F4, F7, F8, T3, T4, T5, T6, C3, C4, P3, P4, O1, O2, Fz, Cz, and Pz). All leads were referenced to linked mastoids (A1 and A2), and a ground electrode was applied to the forehead. Additionally, vertical eye movements were recorded via electrodes placed above and below the left eye. Electrode impedance was maintained below 5 k Ω . The digital EEG data acquisition and analysis system (SynAmps RT) had a band pass of 0.15–100.0 Hz. At cut off frequencies the voltage gain was approximately -6 dB. The 19 EEG traces were digitized online at 1000 Hz with a gain of $10\times$ (accuracy of 29.80 nV/LSB in a 24 bit A to D conversion), and stored on a hard disk.

Two minutes of resting EEG data (with eyes closed) was extracted to determine theta–gamma coupling coefficients. Band pass filtering in combination with a Hilbert transform was used to compute envelopes of the EEG signal. The signal was filtered (Hamming filter; filter order [FO]: 4096) in sequential bands for theta (4–5 Hz, 5–6 Hz, ... 8–9 Hz) and gamma (25–26 Hz, 26–27 Hz, ... 47–48 Hz) oscillations. Digital filtering was performed forward and backward in time in order to eliminate phase shifts. The envelope of each theta band was correlated (Pearson's r) with the envelope of each gamma band. The highest positive correlation between the envelopes of theta and gamma frequency bands was then defined as the characteristic coupling value in each channel for a given subject (Bekisz & Wróbel, 1999; Kamiński et al., 2011; Wróbel, Ghazaryan, Bekisz, Bogdan, & Kamiński, 2007). EEG data was processed using EEGLAB toolbox (freely available from HYPERLINK <http://www.sccn.ucsd.edu/eeglab/>) for MATLAB (The MathWorks, Natick, MA, USA). As stressed by Kamiński et al. (2011), the advantage of this method over looking for peaks within the spectrum is that it directly measures functional coupling between frequency bands in each channel. The coupling values were collapsed over different electrode locations, distinguishing between the hemispheres as well as between frontal, central and parieto-occipital brain areas. The electrode positions were aggregated as follows: frontal left (Fp1, F3, F7), frontal right (Fp2, F4, F8), central left (T3, C3), central right (T4, C4), parieto-occipital left (T5, P3, O1), and parieto-occipital right (T6, P4, O2).

2.2. Results and discussion

The relationship between theta–gamma cross-frequency coupling and IQ scores was determined with Pearson's correlation coefficients. As can be seen in Table 2 theta–gamma cross-frequency coupling, collapsed over different electrode positions, correlated with IQ scores in bilateral frontal and parieto-occipital areas. Verbal IQ scores (VIQ) correlated with theta–gamma coupling in bilateral parieto-occipital areas. On the other hand, performance IQ (PIQ) correlated with theta–gamma coupling in bilateral frontal areas and the left parieto-occipital area, with a trend towards significance in the right parieto-occipital area. Intrasubject variability of theta–gamma cross-frequency coupling coefficients between 19 EEG channels, measured in terms of standard deviation, also correlated with IQ ($r = -0.23, p = 0.02$), PIQ ($r = -0.21, p = 0.04$), and VIQ ($r = -0.20, p = 0.05$). Greater variability of

Table 1
Descriptive statistics for male and female subsamples.

IQ	Male ($n = 50$)	Female ($n = 50$)
<i>M</i>	106.23	106.25
<i>SD</i>	9.86	9.91
Min/max	89–133	87–131
Skewness	0.133	0.176
Kurtosis	0.102	0.189
Shapiro–Wilk test of normality	0.972 $p = 0.234$	0.989 $p = 0.314$

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