

## Short-term memory capacity ( $7 \pm 2$ ) predicted by theta to gamma cycle length ratio

Jan Kamiński<sup>a,\*</sup>, Aneta Brzezicka<sup>b</sup>, Andrzej Wróbel<sup>a</sup>

<sup>a</sup>Nencki Institute of Experimental Biology, Department of Neurophysiology, Warsaw, Poland

<sup>b</sup>Interdisciplinary Center for Applied Cognitive Studies, Warsaw School of Social Sciences and Humanities, Warsaw, Poland

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### ABSTRACT

The number of items that can be held in human short-term memory (STM) is limited to  $7 (\pm 2)$  elements. Lisman and Idiart's theoretical model of STM proposes that this value depends on the number of gamma cycles that can fit in one theta cycle. Previous studies on animals and humans provided support for this hypothesis but direct evidence from human EEG scalp recordings has not previously been reported. We recorded spontaneous EEG activity from 17 participants and measured their verbal STM capacity with a modified digit span task from the Wechsler battery. The strong and positive correlation we found between verbal STM capacity and theta/gamma cycle length ratio thus provides a direct argument in favor of this STM theoretical model. In this study we also demonstrated a new method for assessing individual theta and gamma frequencies by detecting functional coupling between these oscillations.

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### 1. Introduction

The number of items that can be held in human short-term memory (STM) is limited to  $7 (\pm 2)$  elements (Miller, 1956). Lisman and Idiart (1995) proposed a neuronal model of STM in which the number of items that can be memorized without interference is limited by the number of gamma cycles that can fit in one theta cycle. This model posits that memorized items are serially activated in sequential gamma subcycles of one theta period. The involvement of both types of oscillation – theta and gamma – in STM tasks was shown in numerous studies. For example, a systematic increase of theta power with memory load was demonstrated by Jensen and Tesche (2002). This increase was interpreted as an active maintenance and sequential search of STM representation within frontal areas. In another study an increase in the magnitude of frontal theta oscillations and an enhancement of frontal-posterior theta coherence during tasks engaging short-term memory was demonstrated (Sauseng, Klimesch, Schabus, & Doppelmayr, 2005). Increased gamma power during memory load was also reported in subdural recoding on epileptic patients (Howard et al., 2003). Although these studies clearly point to a vital role of theta and gamma oscillations in short-term memory, they do not provide direct evidence for the claim that the STM capacity is limited by the number of gamma cycles within one theta cycle. More straightforward support for the Lisman and Idiart model was published by Axmacher et al. (2010), who in an elegant analysis of intra-hippocampal signals recorded from epileptic patients showed

an increase of gamma amplitude modulation by theta phase during maintenance of face stimuli. It was also shown that successful maintenance of visual information in STM depends on theta and gamma phase synchronization in posterior-parietal recording sites (Sauseng et al., 2009). The present study was designed to further validate the Lisman and Idiart model. For this purpose we used a modified digit span task from the Wechsler battery as a measure of verbal STM capacity and correlated it with individual theta/gamma cycle length ratio for the same subject. Based on the model, we predicted that verbal STM capacity should be strongly correlated with theta/gamma cycle length ratio.

### 2. Materials and methods

Seventeen right-handed adults (seven women) without history of neurological disorders or chronic diseases, aged ( $M = 25.1$ ,  $SD = 3.5$ ), participated in the study. All subjects were volunteers. All participants gave informed consent in accordance with the Ethical Review Board at the Medical University of Warsaw. The EEG signal was recorded from a 64-channel EEG (manufactured by ANT, with sampling rate of 512) during a 5-min session with the subject's eyes closed. After the recording session subjects performed a modified digit span task from the Wechsler battery. In this test, digits were presented visually with an interval of 1 s. The test began with a 3-digit list to remember and ended with a 9-digit list. The number of digits presented during each trial increased by one every two trials. For the analysis, 2 min of EEG signal were taken from resting period with eyes closed from 20 channels of a 10–20 system (Fp1, Fp2, Fp3, F7, Fz, F3, F4, F8, T7, T8, C3, Cz, C4, P7, P3, Pz, P4, P8, O1 and O2).

\* Corresponding author. Address: Nencki Institute of Experimental Biology, Department of Neurophysiology, 3 Pasteura Street, 02-093 Warsaw, Poland.

E-mail address: [j.kaminski@nencki.gov.pl](mailto:j.kaminski@nencki.gov.pl) (J. Kamiński).

Individual frequency bands are traditionally assessed through spectrum analysis. For example Klimesch (1999) proposed that individual theta frequency can be set as a frequency from 4 Hz to 6 Hz beyond individual alpha frequency, defined as a peak in spectrum between 7.5 and 12.5 Hz, whereas Moretti et al. (2009) proposed to define individual gamma frequency as the third peak in spectrum after individual alpha frequency.

The model of STM proposed by Lisman and Idiart (1995) stressed the role of coupled theta and gamma activity during the process of memory maintenance. This prediction was already verified in empirical studies (Axmacher et al., 2010; Sauseng et al., 2009). Unfortunately, the available methods of establishing individual gamma and theta frequencies (see above) do not provide any information about the functional relationship between the two activities, which we believe should be a crucial issue in estimating their mutual ratio.

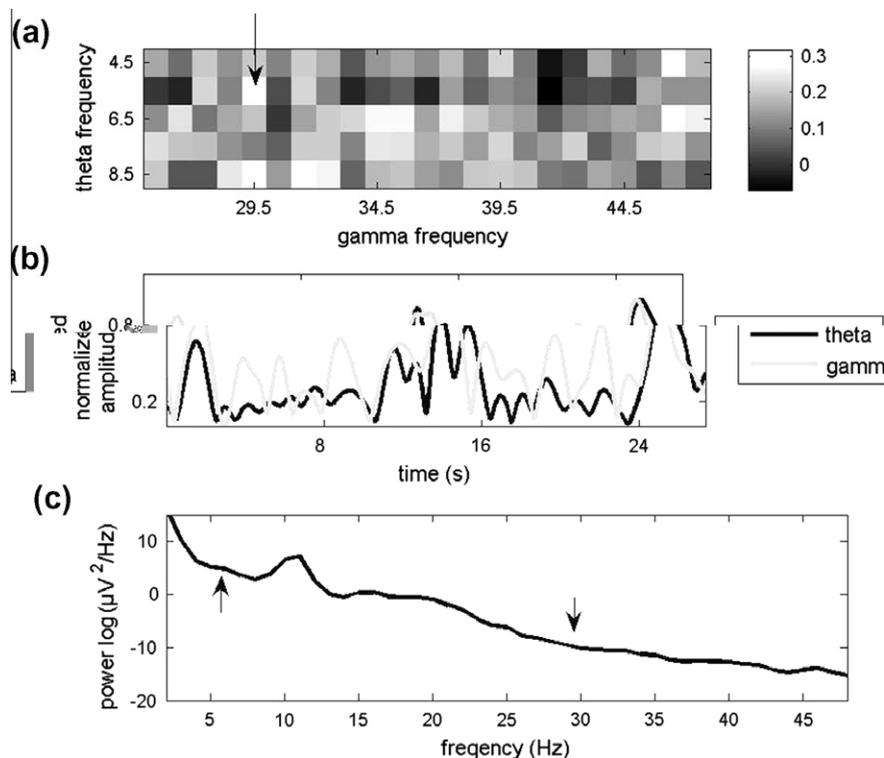
For this reason, in our study we used a new approach for setting individual frequencies for theta and gamma band: the EEG signal was filtered (Hamming filter; filter order [FO]: 4096) in sequential bands for theta (4–5 Hz, 5–6 Hz, ..., 8–9 Hz) and gamma (25–26 Hz, 26–27 Hz, ..., 47–48 Hz) oscillation. Digital filtering was performed forward and backward in time to eliminate phase shifts; examples of filter frequency response are presented in [Supplementary materials](#). The envelope of each theta band was correlated with the envelope of each gamma band. A similar previously successful method was used for coupling measurements between bands (Bekisz & Wróbel, 1999). The two bands with highest positive correlation were then defined as characteristic theta and gamma frequencies for a given subject (see Fig. 1). These individual frequencies were used to calculate the length of theta and gamma cycles and the theta/gamma cycle length ratio. The advantage of

our method over looking for peaks within the spectrum was that it directly measured the functional coupling between bands.

In order to investigate the theta/gamma coupling in more detailed way, we used an earlier proposed measure: “global time of synchrony” (GTS; Wróbel, Ghazaryan, Bekisz, Bogdan, & Kamiński, 2007). In this method we calculated running correlations between theta and gamma envelopes (window 1024 points) and calculated GTS by summing time periods in which the value of correlation exceeded 0.75.

### 3. Results

The correlations between verbal STM capacity and theta/gamma cycle length ratios for all channels are presented in [Table 1](#). It is clearly visible that we observed a significant relationship between these two variables only at the Fz site. The correlation at Fz was strong and highly significant:  $r = 0.79$ ;  $p < 0.001$  (two-tailed test; [Fig. 2](#)). Of all remaining electrodes, the correlation reached a tendency level ( $p = 0.06$ ) only at the F4 site. A similar relation was found also with lower FO used in the filtration process (see [Section 2](#)) but the correlation coefficients were weaker (for FO: 3072,  $r = 0.62$ ;  $p < 0.01$ ; for FO: 2048,  $r = 0.58$ ;  $p < 0.05$ ). The mean value of maximal theta and gamma band correlations for all subjects calculated for 2 min signal at the Fz site was  $r = 0.22$  (SD = 0.04). This correlation was not significantly higher than theta/gamma correlation of signals from other sites (mean correlation on other electrodes was: 0.23; SD = 0.05). In order to check the distribution of these correlations in more detail we performed the “global time synchrony” analysis which showed that the time in which theta/gamma correlation exceeded 0.75 was significantly higher in the signal recorded from the Fz site (17.05 s;

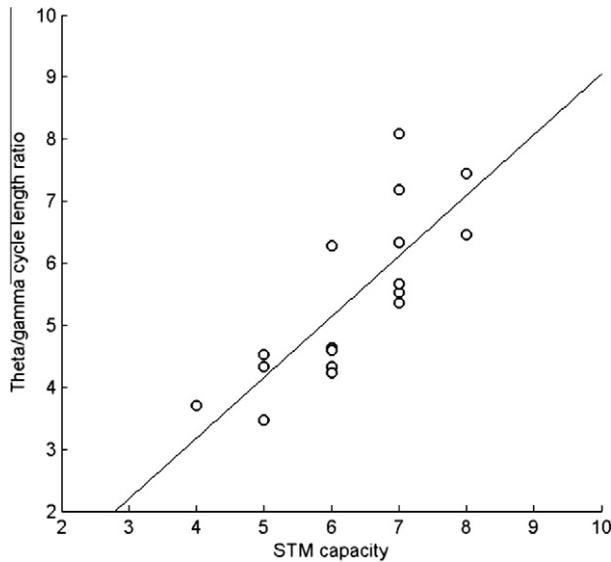


**Fig. 1.** Evaluation of the individual theta and gamma frequencies by envelope correlation at the Fz site (see [Section 3](#)). (a) Matrix of correlation between theta and gamma bands from one subject. Shaded bar to the right indicates correlation value. Arrow points to the value of maximal correlation between bands. (b) Envelope traces of those theta and gamma activity bands which had the highest correlation (indicated by an arrow in 1a). Panel presents 28 s of the signal recorded during period in which the subject had his eyes closed. During this time the correlation reached the value  $r = 0.61$ ,  $p < 0.001$ . (c) Power spectrum of the signal recorded from the same subject for 2 min with eyes closed. There is no trace of an elevated peak within the theta and gamma bands. Arrows point to those frequencies of the theta and gamma bands which exhibited maximal correlation.

**Table 1**  
Correlation between STM capacity and theta/gamma cycle length ratio.

Electrode	Fp1	Fpz	Fp2	F7	F3	Fz	F4	F8	T7	T8
Correlation	-0.43	0.16	0.08	0.04	0.02	0.79***	0.46	0.08	0.31	0.02
Electrode	C3	Cz	C4	P7	P3	Pz	P4	P8	O1	O2
Correlation	0.16	-0.11	0.05	-0.33	0.18	-0.3	0.01	-0.01	0.25	0.45

\*\*\*  $p < 0.001$ .



**Fig. 2.** Scatter plot of STM capacity and theta/gamma cycle length ratio in all subjects. Solid line shows a correlation line.

SD = 5.88 s) as compared to GTS values obtained for other recording sites (mean GTS for other sites was: 11.36 s, SD = 4.6 s with exception of F4, in which GTS, although also higher, did not reach the significance level: 14.35 s; SD = 5.35 s). This result showed that the theta/gamma coupling on frontal sites was uniquely strong as compared to other sites.

The theta/gamma correlations calculated for each subject separately were significant, and could reach higher values for during shorter periods of time (see Fig. 1b). The correlations values for each subject as well as individual theta and gamma cycle lengths are presented in Table 2. Verbal STM capacity did not correlate with age ( $r = -0.31$ ;  $p > 0.05$ ) or education ( $r = -0.2$ ;  $p > 0.05$ ).

**Table 2**  
Maximal correlation between theta and gamma envelopes and cycle length of these bands.

Subject id	Maximal correlation between theta and gamma envelopes	Gamma individual cycle length (ms)	Theta individual cycle length (ms)
1	0.24	21.05	133.33
2	0.22	30.77	133.33
3	0.19	39.22	181.82
4	0.21	33.9	117.65
5	0.19	31.75	117.65
6	0.12	28.99	133.33
7	0.18	25.97	117.65
8	0.18	24.1	133.33
9	0.31	33.9	181.82
10	0.18	28.17	181.82
11	0.27	29.85	222.22
12	0.18	28.99	181.82
13	0.22	23.52	133.33
14	0.27	36.36	153.85
15	0.19	22.47	181.82
16	0.22	30.77	133.33
17	0.25	25.32	181.82

To check whether the theta/gamma correlation could be caused by the narrow filtering process (1 Hz bandpass), we created a signal which had the same statistical properties but did not show a theta/gamma relation. We filtered the signal above and under 20 Hz (with Hamming filter, [FO]: 1024) and shifted the low and high frequency components by a random time interval. We created scrambled signal for each subject and compared theta/gamma relation in real and scrambled signals. The mean correlation between theta and gamma of scrambled signals was near zero (SD = 0.06) and it was significantly lower than the correlation between theta and gamma derived from the real signal at the Fz site ( $t(16) = 9$ ;  $p < 0.001$ ).

In order to check if the relation of verbal STM capacity and theta/gamma cycle length depends on both (theta and gamma) cycle lengths, we performed linear regression with theta and gamma cycle lengths as predictors of individual verbal STM. This analysis showed that both predictors were strong and highly significant (Table 3). As we expected, theta cycle length was positively related to verbal STM capacity whereas gamma cycle length was negatively related. The regression based on these two predictors was significantly better than regression based on theta or gamma cycle length alone. This was proven by performing two hierarchical regression analyses and  $R^2$  change statistics calculations. In the first analysis a theta cycle length was entered as a predictor in a first step and then, in a second step, a gamma cycle length was added to the model. Adding gamma cycle length as a predictor significantly improved the model's predictive power ( $R^2$  change was 0.213, ( $F(1, 14) = 9.27$ ;  $p < 0.01$ ). In the second analysis a gamma cycle length was entered as a predictor in a first step and then, in a second step, a theta cycle length was added to the model. Adding theta cycle length as a predictor improved the model's predictive power over two times more than adding gamma cycle length in the first analysis ( $R^2$  change was 0.537, ( $F(1, 14) = 9.27$ ;  $p < 0.01$ ); ( $F(1, 14) = 23.36$ ;  $p < 0.001$ ). We also checked for any difference between the mean values of verbal STM capacity and theta/gamma ratio. Mean verbal STM capacity was 6.29 (SD = 1.1) whereas mean theta/gamma cycle length ratio was 5.42 (SD = 1.36). The paired  $t$ -test revealed that these two means were significantly different ( $t(16) = 4.35$ ;  $p < 0.001$ ).

We performed additional analysis for alpha (9–10 Hz, ..., 11–12 Hz) to gamma and beta (12–13 Hz, ..., 24–25 Hz) to gamma cycle length ratio at the Fz site to check if these bands also correlate with verbal STM capacity. We did not find any relationship of verbal STM capacity with alpha/gamma cycle length ratio ( $r = -0.37$ ;  $p > 0.05$ ) or beta/gamma cycle length ratio ( $r = -0.38$ ;  $p > 0.05$ ). Although coupling between those band exhibited strength similar

**Table 3**  
Results from liner regression for the STM as a dependent variable.

Predictors	$\beta$	$R^2$
Theta cycle length	0.74***	0.68
Gamma cycle length	-0.46**	

$R^2$  – the proportion of variability in a dependent variable that is accounted for by the statistical model;  $\beta$  – standardized regression coefficient.

\*\*  $p < 0.01$ .  
\*\*\*  $p < 0.001$ .

to the theta/gamma coupling ( $\alpha/\gamma = 0.26$ ,  $SD = 0.05$ ;  $\beta/\gamma = 0.23$ ,  $SD = 0.06$ ).

#### 4. Discussion

This study demonstrated that the theta/gamma cycle length ratio allows for the prediction of subjects' verbal STM capacity. Thus, it provides direct evidence for the theoretical model which proposes that STM capacity is limited by the number of gamma cycles which can fit in one theta cycle (Lisman & Idiart, 1995). We also showed that individual theta and gamma cycle lengths were both significant predictors of verbal STM capacity. The gamma cycle was negatively related to the number of items held in STM, whereas the theta cycle had a stronger and positive impact on verbal STM. We have additionally demonstrated that verbal STM capacity is explained significantly better by combined theta and gamma cycle length than by theta or gamma cycle length alone. Both of these findings are in line with the hypotheses derived from the Lisman and Idiart model. These results were obtained using a specially designed, appropriate method for calculating individual theta and gamma cycle lengths. The method of evaluating characteristic frequencies for each participant individually is theoretically justified and experimentally simple.

As theta power was found to be related to sleepiness (Strijkstra, Beersma, Drayer, Halbesma, & Daan, 2003) and theta frequency shift (in the range of 1 Hz) to motivation (Kasicki, Jeleń, Olszeski, & Sławińska, 2009), it could be argued that subjects' behavioral state could influence the relation obtained in our study. However, the change of theta frequency found in our experiment (from 5 to 13 Hz) was much higher than that reported in those studies. Additionally, we have shown that linear regression with two predictors (theta and gamma cycle lengths) was significantly better than regression based on separate theta or gamma cycle length. This would require a mechanism similar to that predicted by the Lisman and Idiart model to be in operation during the observed process. Thus we believe that the observed theta/gamma dependency is not related to motivational/arousal mechanisms but only to cognitive/perceptual related processes as shown earlier (Griesmayr, Gruber, Klimesch, & Sauseng, 2010).

To check whether the individual frequencies show a pattern of gamma nesting as described by Lisman and Idiart (1995) we ran an additional analysis using the method proposed in Canolty et al. (2006). We did not find any gamma nesting pattern as reported by Canolty et al. (2006) and Axmacher et al. (2010). There are two possibilities for why we did not see gamma amplitude modulation by theta phase. Firstly, those analyses in which such a modulation was observed were conducted on intracranial recordings. It is possible that in EEG recording the nesting pattern was blurred by the scalp and skull tissues. Secondly, it has been shown that gamma nesting on theta phase is higher during STM tasks (Axmacher et al., 2010) and therefore this phenomenon could be even more difficult to observe in relaxed situation.

An important role of theta and gamma interactions in spatial memory has been extensively reported in studies on rat hippocampus. Place cells were shown to fire progressively earlier in theta phase when an animal moves through a place field (O'Keefe and Recce, 1993). This phenomenon, called theta phase precession, is interpreted as a process of recalling a known track from long term memory. The place cells were also shown to continue generation of action potentials locked to the gamma phase at different stages of theta phase precession (Senior, Huxter, Allen, O'Neill, & Csicsvari, 2008). It was proposed that a similar mechanism could be at work also in human STM (Lisman, 2005). Indeed, several studies on human subjects support this theory (Axmacher et al., 2010; Howard et al., 2003; Jensen & Tesche, 2002; Sauseng et al., 2005; Sauseng

et al., 2009). Recent strong evidence came from the experiment of Axmacher and colleagues (2010), who showed that the intertrial variance of theta phase in which gamma amplitude was modulated decreased with STM load. This result was interpreted as an increase in the precision of one-item representation (coded by gamma oscillation) during maintenance of multiple items in STM.

In our study we showed that theta and gamma oscillations are coupled together in ongoing activity. The relation of theta and gamma band oscillation in ongoing activity was also demonstrated in intra cranial recordings in monkeys and humans (Canolty et al., 2006; Lakatos et al., 2005).

We have found a significant relationship between verbal STM capacity and theta/gamma cycle length ratio only on the Fz site. This activity could correspond to frontal medial (FM) theta activity, which reaches maximal amplitude on frontal medial sites (F3, Fz, F4; see Mitchell, McNaughton, Flanagan, and Kirk (2008) for review). FM theta activity has been recently linked to STM by many researchers. For example the increase of FM theta oscillation was demonstrated in Sternberg or N-back tasks (Deiber et al., 2007; Gevins, Smith, McEvoy, & Yu, 1997; Jensen & Tesche, 2002). In a recent EEG study Griesmayr et al. (2010) showed increased cross-frequency phase synchronization between frontal medial theta activity and distributed gamma activity during a task that involved active manipulation of material held in STM. This result demonstrated that FM theta and gamma coupling is not restricted only to passive storage of items in STM but can also be utilized in the active process of holding information in the mind.

The mean value of theta/gamma cycle ratio (5.42) calculated in our experiment was close to (but still significantly lower than) the mean value of STM obtained by digit span task (6.29). Different values of the ratio were reported by Demiralp et al. (2007) in a visual perception task recorded at the O1 site (a value of 6.8) and by Axmacher et al. (2010) in a face maintenance task recorded from the hippocampus (a value of 4.0). These dissimilarities could be caused by different recording sites (frontal vs. occipital vs. intra-hippocampal) and different tasks used in the experiments (ongoing activity vs. visual perception vs. face maintenance). Interestingly, Axmacher et al. (2010) showed a decrease of theta frequency with increasing memory load, which was earlier predicted by one of the variations of the STM model (Jensen & Lisman 1998). On the other hand, data from Axmacher's group (2010) indicated that the frequency ratio between gamma and theta remained constant with increasing memory load, a finding that contradicted the prediction of Jensen and Lisman's model. Our result showing that theta/gamma cycle ratio measured in relaxed situation was significantly lower than STM capacity could indicate that theta/gamma ratios decrease with lower memory load – but this conclusion needs to be further validated.

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#### Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.nlm.2010.10.001.

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