



Alpha-gamma phase amplitude coupling subserves information transfer during perceptual sequence learning

Elinor Tzvi^{a,*}, Leon J. Bauhaus^b, Till U. Kessler^b, Matthias Liebrand^{a,d}, Malte Wöstmann^c, Ulrike M. Krämer^{a,b}

^a Dept. of Neurology, University of Lübeck, Germany

^b Institute of Psychology II, University of Lübeck, Germany

^c Institute of Psychology I, University of Lübeck, Germany

^d Graduate School for Computing in Medicine and Life Sciences, University of Lübeck, Germany

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ABSTRACT

Cross-frequency coupling is suggested to serve transfer of information between wide-spread neuronal assemblies and has been shown to underlie many cognitive functions including learning and memory. In previous work, we found that alpha (8–13 Hz) – gamma (30–48 Hz) phase amplitude coupling ($\alpha\gamma$ PAC) is decreased during sequence learning in bilateral frontal cortex and right parietal cortex. We interpreted this to reflect decreased demands for visuo-motor mapping once the sequence has been encoded. In the present study, we put this hypothesis to the test by adding a “simple” condition to the standard serial reaction time task (SRTT) with minimal needs for visuo-motor mapping. The standard SRTT in our paradigm entailed a perceptual sequence allowing for implicit learning of a sequence of colors with randomly assigned motor responses. Sequence learning in this case was thus not associated with reduced demands for visuo-motor mapping. Analysis of oscillatory power revealed a learning-related alpha decrease pointing to a stronger recruitment of occipito-parietal areas when encoding the perceptual sequence. Replicating our previous findings but in contrast to our hypothesis, $\alpha\gamma$ PAC was decreased in sequence compared to random trials over right frontal and parietal cortex. It also tended to be smaller compared to trials requiring a simple motor sequence. We additionally analyzed $\alpha\gamma$ PAC in resting-state data of a separate cohort. PAC in electrodes over right parietal cortex was significantly stronger compared to sequence trials and tended to be higher compared to simple and random trials of the SRTT data. We suggest that $\alpha\gamma$ PAC in right parietal cortex reflects a “default-mode” brain state, which gets perturbed to allow for encoding of visual regularities into memory.

1. Introduction

Learning a complex new skill requires integration of various cognitive processes on multiple levels of representation. For example, learning to play a guitar song could be implemented by memorizing a motor sequence of finger positions and by perceptually learning the notes on a music sheet. Sequence learning serves as a basis for many skills we perform on a daily basis and has been commonly studied using the serial reaction time task (SRTT; Nissen & Bullemer, 1987). In the standard SRTT, subjects implicitly learn a sequence of motor responses by following a specific pattern of visual stimuli. Thus, sequence learning may be implemented on different levels too: by perceptually learning associations between successive stimuli (S-S associations), or by learning associations between successive responses (R-R associations). Most likely, both kind of associations develop in parallel and

thus contribute to sequence learning by integrating information across domains (Abrahamse, Jimenez, Verwey, & Clegg, 2010).

On the neural level, Hikosaka, Nakamura, Sakai, and Nakahara (2002) proposed that learning a motor skill requires integration across multiple neural networks, each contributing to a certain learning domain. Specifically, motor learning involves a network of motor regions in the basal ganglia, cerebellum and the motor cortex, whereas perceptual learning involves associative areas of basal ganglia and cerebellum together with prefrontal and parietal cortex.

In previous work (Tzvi, Munte, & Kramer, 2014), we implemented a paradigm that disentangles motor from perceptual learning using functional magnetic resonance imaging (fMRI). We found evidence for effective connectivity from M1 to cerebellum underlying implicit motor sequence learning in the SRTT. Next, we used electroencephalography (EEG) to investigate electrophysiological signatures of cortical network

* Corresponding author at: Dept. of Neurology, University of Lübeck, Ratzeburger Allee 160, 23538 Lübeck, Germany.
E-mail address: elinor.tzvi@neuro.uni-luebeck.de (E. Tzvi).

interactions in the SRTT (Tzvi, Verleger, Munte, & Kramer, 2016). We were particularly interested in cross-frequency coupling, which has been shown to underlie learning and memory functions (Fell & Axmacher, 2011) and to serve as a marker for network communication (Canolty & Knight, 2010). We expected to find increased cross-frequency coupling in cortical regions known to be involved in sequence learning. One variant of cross-frequency coupling is phase amplitude coupling (PAC), in which the amplitude of a faster oscillation, e.g., gamma (> 30 Hz), is coupled to a specific phase of a slower oscillation, e.g., alpha (8–13 Hz). PAC has been proposed to coordinate neural processing by gating local neural activity, reflected in high-frequency oscillations, through a temporal window of a low-frequency oscillation (Canolty & Knight, 2010). In our previous EEG study (Tzvi et al., 2016), we found that alpha oscillations play a significant role in implicit visuo-motor sequence learning. Alpha power was modulated in occipito-parietal areas and learning led to reduced cross-frequency coupling of alpha and gamma oscillations over fronto-parietal cortex.

What is the functional role of alpha oscillations in learning? Studies of visuospatial attention showed that posterior alpha power is strongly suppressed contralateral to the attended visual hemifield relative to ipsilateral sites shortly before target onset (e.g. Sauseng et al., 2005). Haegens, Handel, and Jensen (2011) showed that prestimulus alpha decrease is evident not only over visual areas but also in the somatosensory system using a tactile discrimination task. Similarly, in working memory tasks, posterior alpha power during retention decreases contralateral to the attended visual hemifield and increases ipsilaterally (Sauseng et al., 2009). The pre-stimulus decrease in alpha power has been shown to facilitate cortical excitability (Romei et al., 2008). This led researchers to hypothesize that a reduction in alpha power promotes the release from inhibition imposed by alpha oscillations (Jensen & Mazaheri, 2010). Thus, it seems that alpha oscillations may drive both engagement and disengagement of task-relevant and irrelevant regions.

The amplitude/power of an oscillation may however only be part of the story. Studies have shown that the phase of an oscillation, i.e. the current position in a given oscillatory cycle, may provide a temporal code for neural activity and thus influence information flow (Fries, 2005; Palva & Palva, 2011). For example in working memory studies, alpha phase-locking was stronger over occipito-parietal areas, shortly after stimulus onset, for items that had to be memorized (Freunberger, Fellinger, Sauseng, Gruber, & Klimesch, 2009) and when the memory load was increased (Schack, Klimesch, & Sauseng, 2005; Haenschel, Linden, Bittner, Singer, & Hanslmayr, 2010). Phase coupling across electrodes, so called phase synchronization, has been suggested to underlie neural communication essential for working memory as well as long-term memory and learning (Fell & Axmacher, 2011). In a working memory task, load-dependent theta/alpha phase coupling in a fronto-parietal network was most pronounced during the retention period (Schack et al., 2005), suggesting that alpha phase synchronization plays a role in integrating information between remote brain regions. The contribution of alpha-gamma coupling to successful retention was demonstrated in a memory task in which subjects had to either remember or not-remember pictures of landscapes and buildings (Park et al., 2016). In a cue period just prior to stimulus presentation, stronger alpha-gamma phase amplitude coupling ($\alpha\gamma$ PAC) was found in posterior regions for pictures which had to be remembered. Importantly, this was paralleled by an alpha power decrease, suggesting that alpha phase contribution to memory mechanisms is different from alpha power. The authors interpreted these findings to reflect integration between feed-forward and feed-back signals facilitating top-down control (Park et al., 2016).

In this study, we directly follow up on our previous findings relating alpha power and $\alpha\gamma$ PAC to sequence learning in the SRTT. Previously, we found learning-related decrease in $\alpha\gamma$ PAC during visuo-motor sequence learning over bilateral frontal cortex and right parietal cortex. Two alternative interpretations could explain these results. First, $\alpha\gamma$ PAC

might represent interactions in the fronto-parietal network which governs stimulus-response mapping. Once the visuo-motor sequence is encoded into memory, there is less demand for stimulus-response mapping compared to random blocks and therefore $\alpha\gamma$ PAC is reduced. Alternatively, $\alpha\gamma$ PAC might represent a “default mode” brain state which is reduced when encoding a sequence. This explanation dovetails with the “desynchronization hypothesis” recently put forth by Hanslmayr, Staudigl, and Fellner (2012). They hypothesize that information encoding into memory systems benefits from oscillatory desynchronization as it increases the entropy, i.e., the richness of the information. Based on this theory, investigating $\alpha\gamma$ PAC during “resting state” could provide further evidence for the specificity of $\alpha\gamma$ PAC reduction during sequence learning, thus rejecting claims of unspecific $\alpha\gamma$ PAC effects related to task complexity.

Here, we tested predictions derived from these alternative explanations in a purely perceptual version of the SRTT (Rose, Haider, Salari, & Buchel, 2011). Based on the “stimulus-response mapping” explanation, we predict that (i) $\alpha\gamma$ PAC is reduced only once the sequence has been learnt, (ii) $\alpha\gamma$ PAC in fronto-parietal cortex remains unchanged compared to random trials when learning a purely perceptual sequence as it does not decrease the demands for mapping the visual stimuli onto the motor responses, and (iii) $\alpha\gamma$ PAC should be lowest under minimal stimulus-response mapping demands. Alternatively, the “default-mode” explanation would predict that (i) $\alpha\gamma$ PAC is reduced while learning, (ii) fronto-parietal $\alpha\gamma$ PAC should be reduced when encoding the perceptual sequence and (iii) fronto-parietal $\alpha\gamma$ PAC should remain unchanged under minimal stimulus-response mapping demands as no encoding of a sequence takes place. To test these hypotheses, participants performed in a purely perceptual sequence learning SRTT (Rose et al., 2011). The task entailed long sequence blocks in which the perceptual sequence was repeated 10 times to facilitate learning. These blocks were preceded and followed by shorter random blocks with no specific pattern of any kind. We also implemented a condition that required no stimulus-response mapping. We hypothesized that if the “stimulus-response mapping” theory is correct, $\alpha\gamma$ PAC should be lowest for this condition, whereas the “default mode” explanation would suggest that $\alpha\gamma$ PAC should be highest in this condition. Finally, we used “resting-state” data of a separate cohort to test the “default mode” theory. If this theory is correct, fronto-parietal $\alpha\gamma$ PAC should be reduced when encoding the perceptual sequence compared to “resting-state”.

Finally, with respect to condition differences in oscillatory power, we expected posterior alpha power to be decreased, reflecting recruitment of occipito-parietal areas when encoding the perceptual sequence. As alpha phase synchronization was suggested to serve as a marker for inter-regional communication, we expected that reduced alpha phase coupling during learning would be evident in electrodes that show reduced $\alpha\gamma$ PAC.

2. Methods

2.1. Study 1: Serial reaction time task

2.1.1. Participants

Twenty-five healthy participants (mean age: 23 years, range 19–28; 20 females) took part in the experiment after giving informed consent. All participants were right handed, had normal or corrected to normal vision with no color deficiency. The study was approved by the Ethics Committee of the University of Lübeck and was performed in accordance with the Declaration of Helsinki. We excluded one participant due to an error in data acquisition. For the behavioral analysis, two participants were excluded after making more than 50% errors. For the EEG data analysis, an additional participant was excluded due to artifacts in the analyzed electrodes resulting in a total sample of 21 participants.

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