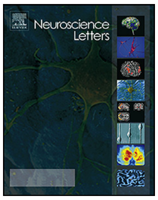
Neuroscience Letters 558 (2014) 73–77

Contents lists available at ScienceDirect

Neuroscience Letters

journal homepage: www.elsevier.com/locate/neulet



Dynamic cortical involvement in implicit anticipation during statistical learning

Mario Altamura[a,e,*], Frederick W. Carver[d], Brita Elvevåg[a], Daniel R. Weinberger[a,b,c], Richard Coppola[a,d]

[a] Clinical Brain Disorders Branch, NIMH, Building 10, Bethesda, MD 20892, USA
[b] Lieber Institute for Brain Development, Baltimore, MD 21205, USA
[c] Department of Psychiatry, Neurology, Neuroscience, and the Institute of Genetic Medicine, Johns Hopkins University School of Medicine, Baltimore, Maryland 21205, USA
[d] MEG Core Facility, NIMH, Building 10, Bethesda, MD 20892, USA
[e] Department of Clinical and Experimental Medicine, Psychiatry Unit, University of Foggia, Foggia, Italy

HIGHLIGHTS

- Development of the prediction of future events during implicit statistical learning.
- Study is conducted using a neuroimaging technique with high temporal resolution: MEG.
- The spatiotemporal distribution of ERD/ERS is identified.
- Anticipatory behavior involves motor and perceptual anticipation at different time points.

ARTICLE INFO

Article history:
Received 13 June 2013
Received in revised form 4 September 2013
Accepted 19 September 2013

Keywords:
Implicit learning
Anticipatory processes
Motor anticipation
Perceptual anticipation
Electroencephalography

ABSTRACT

The prediction of future events is fundamental in a large number of critical neurobehavioral contexts including implicit motor learning. This learning process relies on the probabilities with which events occur, and is a dynamic phenomenon. The aim of present study was to investigate the development of anticipatory processes during implicit learning. A decision making task was employed in which the frequency of trial types was manipulated such that one trial type was disproportionately prevalent as compared to the remaining three trial types. A 275 channel whole-head magnetoencephalography (MEG) system was used to investigate the spatiotemporal distribution of event-related desynchronization (ERD) and synchronization (ERS). The results revealed that oscillations within the alpha (10–12 Hz) and beta (14–30 Hz) frequencies were associated with anticipatory processes in distinct networks in the course of learning. During early phases of learning the contralateral motor cortex, the anterior cingulate, the caudate and the inferior frontal gyrus showed ERDs within beta and alpha frequencies, putatively reflecting preparation of next motor response. As the task progressed, alpha ERSs in occipitotemporal regions and putamen likely reflect perceptual anticipation of the forthcoming stimuli.

1. Introduction

The ability to extract regularities embedded in a random sequence of events plays a central role in human cognition. Behavioral evidence suggest that the process through which people become sensitive to regularities in the environment is automatic and occurs implicitly in the absence of awareness that one is learning [5]. In everyday situations many events follow one another on a probabilistic way rather than according to a fully predictable pattern. Studies of statistical learning processes have employed probabilistic sequential paradigms in which certain sequences of trials occur more frequently than others but do not follow a fixed sequence of events. In those studies the improvement of performance for stimuli that are highly frequent as compared to less frequent indicated that people implicitly learn statistical regularities [15,20]. The mechanisms underlying implicit learning are not fully understood, but most evidence suggests that an important process is the development of an automatic prediction of upcoming events based on the extracted regularities [10,12,17]. This has been especially true during implicit statistical learning [9,21].

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[*] Corresponding author at: Department of Clinical and Experimental Medicine, Psychiatry Unit, University of Foggia, Foggia, Italy. Tel.: +39 0881732285; fax: +39 0881732285.
E-mail address: m_altamura@virgilio.it (M. Altamura).

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http://dx.doi.org/10.1016/j.neulet.2013.09.043

However, though the ability to predict future events during implicit learning is well established, little is known about the brain circuits underling the development of such predictive processes. It has been suggested that implicit learning involves anticipation and preparation of the next motor response [6,10]. A recent neuroimaging study demonstrated that the medial temporal lobe and perceptual anticipation in visual areas play a critical role during implicit statistical learning [21]. However, the relatively poor temporal resolution of neuroimaging methods makes it difficult to track the subsecond time course of activation in different brain areas as people anticipate an upcoming stimulus. It has been suggested that implicit learning relies on the dynamic involvement of different brain areas over time suggesting that with experience people are increasingly able to make predictions about future events during the course of learning [3,13,19]. Therefore, it is conceivable that different sets of cortical regions are dynamically involved in implicit anticipation triggered by statistical learning. In the current study, we employed a neuroimaging technique with superior spatiotemporal resolution – magnetoencephalography (MEG). Event-related oscillatory responses can be quantified using the event-related desynchronization/synchronization method in which a relative decrease in the power in specific frequency bands during information processing is called event related desynchronization (ERD) and a relative increase in the power is called event-related synchronization (ERS). We adapted a Stroop-like task that we have previously employed [7]. Unbeknownst to the participants the frequency with which various trial types occurred was manipulated, such that one trial type was disproportionately prevalent in comparison to the other trial types. The aim of the current study was to evaluate the spatio-temporal proprieties of anticipatory oscillatory activity with regard to frequency of stimulus exposure, the progressive modulation of anticipatory oscillatory activity over time for the different exposure conditions, and to study whether possible anticipatory activity in specific brain regions was related to a change in behaviors. Based on previous results we expected that participants would exploit past experience with the statistical structure of stimulus sequences for successful anticipation of upcoming events. We predicted that motor as well visual regions might contribute to the formation of anticipatory behavior and the adjustment of participants' predictions and anticipation over the course of the experiment. Previous studies have repeatedly demonstrated that activity changes within the alpha band (8–12 Hz) can be used as an indicator of localized brain activation in motor and visual regions in a variety of cognitive tasks including implicit learning [2,24]. We predicted that power changes in alpha may reflect anticipation of forthcoming stimuli to the extent to which participants had learned the predictability of the highly frequent stimuli. To test the specificity of the effects of anticipatory behavior on alpha band oscillations, additional frequency ranges were also included in our analysis.

Participants: Eight healthy volunteers (4 women, 4 men; mean age 29.76; SD = 5.82) participated in this study. All participants were right handed native English speakers. None of the participants had a history of neurological or psychiatric disease. Informed written consent was obtained from all participants. The study was in accordance with the Helsinki Declaration and it was approved by the National Institute of Mental Health Institutional Review Board.

Behavioral procedures: Participants were presented with a series of trials, each of which consisted of images of two animals of different sizes that were presented side by side on a computer monitor. In all trials, one image appeared larger than the other. The size of the animal images was either congruent or incongruent with the relative size in the real world. For example, a congruent stimulus was an image of a large elephant next to an image of a small ant, while an incongruent stimulus was an image of a large ant next to an image of a small elephant. Participants were instructed to press one of two buttons with their right hand to indicate which animal was larger in the real world, either the one on the left or the one on the right. The animal pairs were presented for 1 s, followed by an inter-trial interval in which a crosshair was presented for 1 s. Therefore, each trial lasted for 2 s. There were 300 trials in total, thus the entire experiment lasted for 10 min. We presented a disproportionately large number of trials (60%) with the larger, congruently sized animal appearing on the left side of space (congruent left). The other three trial types (congruent right, incongruent left, incongruent right) equally comprised the remaining 40% of the trial types. The trials were pseudo-randomized so that the probability rules (60% of the congruent left trial type and 40% of the other trial types) held in each successive quarter set of 75 trials each. No more than three of the similar type were consecutively presented. Participants were given no information about the rules by which the series of trials was constructed. They saw the series of trials presented one after the other without interruptions. To test the implicitness of learning participants were debriefed after the experiment.

Image acquisition procedures: MEG signals were recorded in a magnetically shielded room using a helmet-shaped CTF 275-channel whole head system (CTF Systems Inc.) at a sampling rate of 600 Hz. Stimuli were presented to subjects via Presentation® software (www.neurobs.com). The computer image was projected onto a screen 60 cm in front of the subject's eyes. For each person, a series of volumetric MRI scans was co-registered with their MEG head coordinate system. Anatomical MRI scans were obtained using a 1.5 Tesla GE scanner.

Data analysis: The raw data were filtered in 3rd gradient mode for noise reduction along with DC offset removal and high-pass filtering at 0.61 Hz. The presence of an adequate MEG signal was determined by visual inspection of the raw signal and trials that contain artifacts were rejected. The data were divided into four frequency bands: theta (5–8 Hz), lower alpha (8–10 Hz), upper alpha (8–12 Hz), beta (14–30 Hz), and gamma (30–50 Hz). As the principal interest in the present study was the prediction that the time course of the activation in the brain regions would differ at the beginning of the experiment as compared to the end, the most frequent trial type of congruent left were split into quarters of 75 trials each so as to index change across time. To achieve equality of frequencies of occurrence of the most frequent trials in each of successive quarter and the less frequent trials we compared each quarter of the most frequent trial type (congruent left) to all the trials of the less frequent trial type (congruent right). We chose the congruent right stimulus type because congruency was held constant; the only difference being the prevalence with which it was presented and which button was the correct response.

Synthetic aperture magnetometry (SAM): SAM was used to reconstruct topographical maps of brain source power from band-limited MEG data [23]. A calculation of source power was performed for 7.5 mm^3 voxels throughout the brain volume. For each participant, the SAM image was normalized to *Z*-scores by the pooled variance across the volume. For analysis of brain activity, only trials on which responses were correct were included. To define the spatiotemporal sequence of those cerebral regions active during different phases of the experiment SAM analysis were performed on the active epoch from −500 ms before the onset of the imperative stimulus to +1000 ms after stimulus onset. Trials were segmented using a sliding 300 ms time window moved with 100 ms increments. The reference interval of 300 ms was epoched from the inter-trial interval starting −800 to −500 ms before stimulus onset. The amplitude was obtained by computing a pseudo-*F* ratio between the power in the active and the reference interval. Band power changes were expressed as the percentage of a decrease (ERD) or increase