



Expected reward modulates encoding-related theta activity before an event

Matthias J. Gruber ^{a,*}, Andrew J. Watrous ^b, Arne D. Ekstrom ^b, Charan Ranganath ^b, Leun J. Otten ^a

^a Institute of Cognitive Neuroscience, University College London, 17 Queen Square, London WC1N 3AR, UK

^b Center for Neuroscience, University of California at Davis, 1544 Newton Court, Davis, CA 95618, USA

ARTICLE INFO

Article history:

Accepted 25 July 2012

Available online 16 August 2012

Keywords:

Prestimulus activity

Memory encoding

Reward

Theta

Anticipation

Long-term memory

ABSTRACT

Oscillatory brain activity in the theta frequency range (4–8 Hz) before the onset of an event has been shown to affect the likelihood of successfully encoding the event into memory. Recent work has also indicated that frontal theta activity might be modulated by reward, but it is not clear how reward expectancy, anticipatory theta activity, and memory formation might be related. Here, we used scalp electroencephalography (EEG) to assess the relationship between these factors. EEG was recorded from healthy adults while they memorized a series of words. Each word was preceded by a cue that indicated whether a high or low monetary reward would be earned if the word was successfully remembered in a later recognition test. Frontal theta power between the presentation of the reward cue and the onset of a word was predictive of later memory for the word, but only in the high reward condition. No theta differences were observed before word onset following low reward cues. The magnitude of prestimulus encoding-related theta activity in the high reward condition was correlated with the number of high reward words that were later confidently recognized. These findings provide strong evidence for a link between reward expectancy, theta activity, and memory encoding. Theta activity before event onset seems to be especially important for the encoding of motivationally significant stimuli. One possibility is that dopaminergic activity during reward anticipation mediates frontal theta activity related to memory.

© 2012 Elsevier Inc. All rights reserved.

Introduction

There is growing evidence that, in addition to brain activity that is evoked by an event, brain activity patterns that precede the onset of an event can contribute to memory performance. Several functional magnetic resonance imaging (fMRI) and magneto-/electroencephalography (M/EEG) studies have shown that activity just before initially encountering a new stimulus can predict whether that stimulus will be remembered during a later memory test (Adcock et al., 2006; Bollinger et al., 2010; Fell et al., 2011; Galli et al., 2011; Gruber and Otten, 2010; Guderian et al., 2009; Mackiewicz et al., 2006; Otten et al., 2006, 2010; Padovani et al., 2011; Park and Rugg, 2010; Uncapher et al., 2011). In particular, M/EEG studies have shown that oscillatory activity in the theta (4–8 Hz) frequency band prior to the onset of a study or test item is enhanced on trials for which the item is subsequently remembered (Addante et al., 2011; Fell et al., 2011; Guderian et

al., 2009). These findings suggest that theta activity can set the stage for effective encoding and retrieval. However, it is largely unknown what factors influence such prestimulus theta activity.

Studies in rodents suggest that reward may be one factor that contributes to theta activity (Benchenane et al., 2010; van Wingerden et al., 2010). For instance, van Wingerden et al. (2010) found that firing of neurons in the orbitofrontal cortex of rats showed increased theta phase locking during anticipation of a reward. In humans, reward motivation has been linked to successful memory encoding (Adcock et al., 2006; Wittmann et al., 2005), suggesting that there might be a relationship between reward expectancy, anticipatory theta activity, and memory encoding in humans.

To test this possibility, we took advantage of a data set previously only considered in terms of event-related potentials (Gruber and Otten, 2010). Oscillatory theta power was extracted from scalp-recorded electrical brain activity obtained during intentional memorization of words (cf. Adcock et al., 2006). Each word was preceded by a low or high reward cue, which indicated the amount of money that would be earned if the word was remembered in a later recognition test. Rewards were delivered at the end of the experiment. The analyses focused on theta power in the interval between the reward cue and word onset. The question of interest was whether theta activity before word onset (hereafter referred to as

* Corresponding author at: Center for Neuroscience, University of California at Davis, 1544 Newton Court, Davis, CA 95618, USA. Fax: +1 530 757 8640.

E-mail address: mjgruber@ucdavis.edu (M.J. Gruber).

'prestimulus' activity) would predict subsequent memory of the word and, if so, whether this activity would differ between low and high reward cues.

Methods

Participants

The experimental procedures were approved by the University College London Research Ethics Committee. The analyses reported here are based on a subset of twenty participants in Gruber and Otten (2010) who had at least twelve artifact-free remembered and forgotten trials in either the high or low reward condition (for details, see the *Statistical analyses* section). Participants (mean of age 24 years; range of 19–33 years; 7 men) were right-handed, had normal or corrected-to-normal vision, and reported not to have had any neurological or psychiatric illnesses. All participants provided informed written consent before participating.

Procedure

Participants completed an intentional memorization task (Fig. 1), followed by a recognition memory test after a delay of about 15 min. Stimuli consisted of a series of 4–8 letter visually-presented words with a written frequency of 1–30 per million (Kučera and Francis, 1967). Each study trial commenced with the presentation of a low ('20p' written in black) or high (£2' written in green) monetary reward cue 2 s before word onset. The cue was presented for a duration of 1 s and was replaced by a fixation cross for the remaining 1 s of the cue-word interval. The study sequence consisted of 120 low and 120 high randomly intermixed reward cues. Words were shown for 0.5 s followed by a fixation cross until the next cue. The time between word onset until the next cue varied randomly between 4 and 5.5 s. Participants were told that the cue represented the amount of additional money they would receive at the end of the experiment if they successfully recognized the upcoming word in the later memory test. Participants received 5% of their total earnings on top of the hourly reimbursement rate. In addition to memorizing the words, participants also had to indicate whether the first and last letters of a word were in alphabetical order to ensure attention was paid to all words.

All 240 studied words were shown again in the recognition memory test, intermixed with 120 new words. Each test trial commenced with the presentation of a neutral warning stimulus ('!') for 1 s, followed by the presentation of the test word for 0.5 s. The interval between successive warning stimuli varied randomly between 4 and 5.5 s. The memory test incorporated a five-way recognition confidence judgment

(Yonelinas et al., 2005). Participants pressed one of five buttons to indicate that they (i) recollected specific details about the word's initial occurrence (a 'remember' response), (ii) were confident about the word's earlier occurrence without further details (a 'confident old' response), (iii) thought that they recognized the word (an 'unconfident old' response), (iv) thought the word was new to the experiment ('unconfident new'), or (v) were confident that the word had not been presented earlier (a 'confident new' response). The time–frequency analyses focused on the comparison between studied items later confidently judged as old (i.e. given a 'remember' or 'confident old' response) and items later incorrectly judged as new (i.e. given an 'unconfident new' or 'confident new' response). Insufficient trials were available to split these categories further. Rewards were provided for any correctly recognized old word, regardless of the type of judgment associated with the decision. False alarms attracted a £2.50 penalty to discourage participants from saying 'old' all the time.

EEG acquisition and time–frequency analyses

Electrical brain activity was recorded during the memorization task with sintered silver/silver-chloride electrodes attached to 34 scalp sites (montage 10 at [www.easycap.de/e/electrodes/13_M10.htm](http://www.easycap.de/easycap/e/electrodes/13_M10.htm)) referenced to the midfrontal site Fz. Vertical and horizontal eye movements were recorded from electrodes above and below the right eye and at the outer canthi, respectively. Signals were digitized at 500 Hz and filtered with a bandpass between 0.01 and 35 Hz.

The EEGLAB toolbox (Delorme and Makeig, 2004) was used to pre-process the EEG data and conduct time–frequency analyses. The continuous EEG was high-pass filtered with a cut-off at 0.5 Hz and divided into epochs ranging from 600 ms before cue onset until 4.2 s thereafter. This epoch length was chosen to derive time–frequency information for the entire 2 s cue-word interval and 1.6 s after word onset. Inclusion of the 600 ms periods at the beginning and end of the epochs was necessary to avoid edge effects in the time periods of interest. Epochs were baseline-corrected in the time domain using the mean signal in the 600 ms period before cue onset. Trials in which EEG activity exceeded more than three standard deviations from the mean on that electrode or five standard deviations across all electrodes were excluded from the analyses. Blinks and eye movements were removed via independent component analysis (Bell and Sejnowski, 1995; Delorme and Makeig, 2004), which has been shown to be an effective way to eliminate such artifacts from EEG (e.g. Hoffmann and Falkenstein, 2008). A final check was performed manually and any trials that contained further muscle artifacts, amplifier saturations or incorrect alphabetic responses were excluded from the analyses. The data were then re-referenced to the average of the left and right mastoids. The online reference at the midline frontal site Fz was reinstated and used as a scalp site of interest.

Time–frequency analyses were conducted using Morlet wavelets (Percival and Walden, 1993) with 4 cycles and a sliding time window which was moved in 10 ms increments in the 0–3.6 s interval. This computation was done in steps of 1 Hz from 4 to 12 Hz. The analyses reported here did not employ a baseline in the frequency domain. Because the focus here was on differences in oscillatory power between trial types, this step was not necessary (cf. Addante et al., 2011; Fell et al., 2011; Guderian, et al., 2009; Mazaheri et al., 2009). An additional analysis using mean frequency power across the epoch as a baseline led to the same conclusions as those reported here. For each participant, EEG data during study trials were binned according to the type of reward cue (low vs. high) and subsequent memory performance (remembered vs. forgotten). Words were classified as remembered when they were given a 'remember' or 'confident old' judgment and as forgotten when they received an 'unconfident new' or 'confident new' judgment. The mean numbers of remembered and forgotten trials were, respectively, 33 and 42 in the low reward

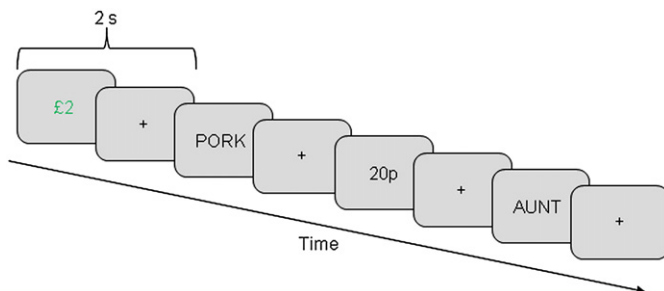


Fig. 1. Experimental procedure of the encoding phase. Each word (e.g. 'pork' or 'aunt') was preceded by either a low or a high reward cue ('20p' written in black or '£2' written in green, respectively). The reward cue indicated the amount of money that would be received if the upcoming item was remembered in a later recognition test. The interval between cue and word was constant (i.e. 2 s) and was used for the analyses of encoding-related theta activity.

Download English Version:

<https://daneshyari.com/en/article/6030956>

Download Persian Version:

<https://daneshyari.com/article/6030956>

[Daneshyari.com](https://daneshyari.com)