Neuroscience Letters 438 (2008) 270–274

Contents lists available at ScienceDirect

Neuroscience Letters

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

Prestimulus EEG alpha activity reflects temporal expectancy

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ARTICLE INFO

Article history:
Received 28 December 2007
Received in revised form 3 April 2008
Accepted 16 April 2008

Keywords:
CNV
Expectancy
Prestimulus alpha activity
Top-down processing

ABSTRACT

Since prestimulus EEG alpha activity has recently been considered to convey prestimulus top-down processing, we investigated whether prestimulus alpha activity reflects temporal expectancy of upcoming stimulation even under the non-classical contingent negative variation (CNV) paradigm. EEG was recorded from 16 subjects performing a color and a shape discrimination task manipulated with constant and variable inter-stimulus interval (ISI) conditions. The power of oscillatory activity was investigated by convolving the EEG signals with Morlet wavelets. The constant ISI condition yielded significantly shorter reaction times than the variable ISI condition, indicating more efficient preparation for upcoming stimuli during the constant ISI. We found significantly higher prestimulus alpha activity in the constant ISI condition than in the variable ISI condition, but no significant CNV even in the constant ISI condition. Such a reflection of temporal expectancy in the prestimulus alpha activity corroborates that the prestimulus top-down mental state for preparing upcoming task-performance is considerably reflected in the prestimulus ongoing alpha activity.

In everyday life, people often anticipate what might possibly occur. Many researchers have sought to find the electrophysiological correlates of anticipation in mental performance. Contingent negative variation (CNV) of event-related potentials (ERPs) has been known to reflect the expectation of a subsequent event prior to a stimulation [2,19,22]. CNV develops slowly before the stimulus onset in a person who is actively predicting the occurrence of some significant stimulus requiring a response.

Additionally, a growing body of evidence has suggested that EEG alpha activity may be involved in higher cognitive functions such as temporal expectancy for upcoming events [7,10,14]. These previous studies on the relationship between alpha activity and expectancy were mostly associated with the classical CNV paradigm, where a pair of contingent stimuli (S1: a warning stimulus, S2: an imperative stimulus) is presented with a distinct time interval [2,22], and such stimulus contingency (temporal association between the two stimuli) allows subjects to predict and prepare for the second stimulus requiring the execution of a response. Until now, most experimental paradigms have been restricted to a considerable extent within the classical CNV paradigm in order to investigate a possible electrophysiological indicator for temporal expectation.

Min and Herrmann [16] recently reported the prestimulus reflection of poststimulus events in human EEG alpha activity and interpreted their results, in a way that prestimulus alpha activity might reflect top-down information in advance of stimulus onset. These results led to the further supposition that alpha activity can reflect expectancy in a more general way. Therefore, we hypothesized that the temporal expectancy of upcoming events could be reflected in alpha activity under more general circumstances even when the classical CNV is undetectable. Consequently, we employed the same experimental paradigm as the study by Min and Herrmann [16] except for the inter-stimulus interval (ISI) condition. Their study used only a variable ISI condition, whereas in the present study we manipulated the ISI condition and compared prestimulus alpha activity depending on the two different types of the ISI condition (a constant ISI versus variable ISIs). Although this experimental paradigm slightly deviated from the classical CNV paradigm, we anticipated that the brain might generate more temporal expectation about the appearance of stimuli it encountered periodically (i.e., during the constant ISI condition) than during the variable ISI condition and that this temporal expectation would be reflected in the prestimulus alpha activity.

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doi:10.1016/j.neulet.2008.04.067

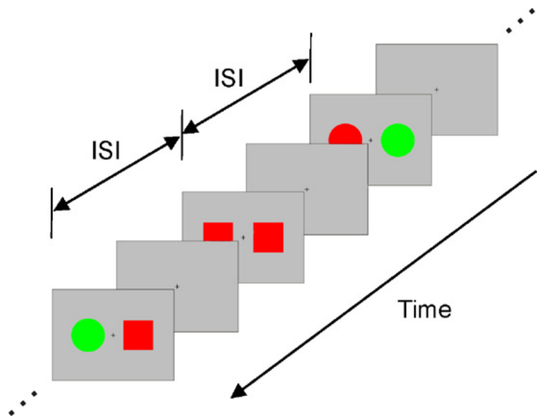

Fig. 1. A schematic task flow shows sample stimuli and the ISIs. Two stimuli randomly drawn from a set of red or green circles or squares were presented bilaterally on a light-gray background on a computer monitor. Stimulus presentation was followed by a fixation cross, which was presented during every ISI. Two types of ISI were employed in the present study: variable ISI and constant ISI. The variable ISIs ranged randomly from 1500 to 2500 ms, whereas 1500 ms was used as a constant ISI. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Sixteen subjects participated in this study (8 females, mean age 23; range 19–28 years) under the local ethics guidelines and the Declaration of Helsinki (World Medical Association: Ethical Principles for Medical Research Involving Human Subjects, 1964). All subjects were free of neurological or psychiatric disorders. All of them had normal or corrected-to-normal vision, and none of them were color-blind (examined by the *Ishihara* color test). Pairs of colored figures randomly drawn from a set of red or green circles or squares were used as stimuli (cf. Fig. 1). The areas of circles and squares were matched. Stimuli were presented on a computer monitor placed at a distance of 1 m in front of the subject for a duration of 500 ms. Two colored figures consisting of a stimulus set were presented bilaterally on a light-gray background at an eccentricity of a 3° visual angle and each colored figure of a stimulus set spanned a 4° visual angle. All types of stimuli appeared pseudorandomly with equal probability. Each stimulus presentation was followed by variable ISIs randomly ranging from 1500 to 2500 ms for the variable ISI condition, and the value of the 1500 ms was used as an ISI for the constant ISI condition. Subjects were asked to remain centrally fixated and were instructed to press a button with the index finger of one hand if the target feature of the task ('color' in the color task and 'shape' in the shape task) was the same and to press a button with the other hand if it was not. In order to induce anticipatory attention of upcoming stimuli, subjects were asked to press the button as quickly as possible. The experiment consisted of two task-sessions: a color task and a shape task. Stimuli in each task were presented in two blocks and were separated by short rest periods in between. Response hands and the order of tasks were counterbalanced across subjects. The experiment consisted of 400 trials for each task. Only trials with correct responses were further analyzed.

EEG was recorded using a GRASS 15A54 amplifier (Grass Technologies, USA) with 21 sintered Au/Ag-electrodes. Their locations, according to the international 10-20 system are as follows: AFz, Fp1, Fp2, Fz, F3, F4, F7, F8, Cz, C3, C4, T3, T4, Pz, P3, P4, T5, T6, Oz, O1 and O2. We also placed an electrode on each mastoid for the linked reference and a ground electrode at nasion. Eye movement activity was monitored with two additional electrodes placed supra-orbitally to both eyes and was referenced to the linked mastoids. Electrode impedances were kept below 10 kΩ prior to data acquisition. EEG was sampled at 1000 Hz (analogue band-pass filter 0.1–100 Hz) and stored for off-line analysis. Data were epoched from 1000 ms prestimulus to 1000 ms poststimulus. Epochs containing eye-movements or other artifacts (maximum amplitude ±70 μV or electrode drifts) were rejected. Two subjects had to be excluded from further analyses because of poor data quality.

To investigate the power of oscillatory activity, the EEG signals were convolved with Morlet wavelets [11,12]. The Morlet-convolved signal shows a Gaussian envelope with a temporal standard deviation (σ_t) and a spectral standard deviation ($\sigma_f = 1/(2\pi\sigma_t)$) around its central frequency (f_0):

$$\Psi(t, f) = A \exp(i2\pi f t) \exp\left(\frac{-t^2}{2\sigma_t^2}\right).$$

In order to have unit energy at all scales, the wavelet functions should be normalized prior to the convolution; for the Morlet wavelet transform, the normalization parameter A is $\sigma_t^{-1/2}\pi^{-1/4}$. A wavelet family is characterized by a constant ratio (f_0/σ_f), and we employed a wavelet family with 7 as its constant ratio [21] and f_0 ranging from 5 to 20 Hz in 1 Hz steps. In the case of 10 Hz, this yields a wavelet duration ($2\sigma_t$) of 222.8 ms and a spectral bandwidth ($2\sigma_f$) of 2.9 Hz around its central frequency (f_0 = 10 Hz).

To avoid cancelling out non-phase-locked activity in the average, each single trial was first wavelet-transformed and these transformed data were subsequently squared for computing power of activity. In other words, the power [P(t, f)] of the signal in a frequency band is the square norm of the result of the convolution of a complex wavelet [$\Psi(t,f)$] with the signal [$s(t)$] [11,21]:

$$\mathrm{P}(t, f) = |\Psi(t, f) \times s(t)|^2.$$

No baseline correction was applied to the alpha activity since activity in a prestimulus period would vanish after baseline correction.

It has been demonstrated that subjects differ considerably in their 'individual alpha frequency (IAF)' [6,13]. Therefore, the frequencies used in the wavelet analyses of alpha activity were determined individually for every subject. Morlet wavelet transforms for oscillatory activity were first computed for the electrode Oz, where the prestimulus power of alpha activity was most pronounced. From this time–frequency scalogram, the IAF was obtained as the maximal power of activity in the frequency range between 8 and 13 Hz in a time window from 250 to 50 ms prior to stimulus onset. This time window was chosen to avoid the temporal smearing of poststimulus activity into the baseline [11] while trying to take the time window as close to the stimulus onset as possible and also to include a reasonable period having more than one cycle of alpha frequency. For obtaining a single IAF irrespective of task-types, we averaged such maxima across both tasks within each subject. The comparison of the prestimulus IAFs between the two ISIs was performed by a paired-samples t-test (two-tailed).

In order to compare the prestimulus alpha power across the two ISI conditions in both tasks, we measured the mean power of the alpha activity of the IAF (each central frequency within a 1-Hz bin with its spectral bandwidth ($2\sigma_f$)) in the time window from 250 to 50 ms prestimulus on the electrode Oz. For the CNV analysis, we performed a baseline correction from 1000 to 900 ms prestimulus on the ERPs and assessed the mean amplitude of ERPs within the time window from 600 to 500 ms prestimulus on the electrode Fz to evaluate the initial CNV (iCNV). This was because the term 'expectancy wave' [22] as used for the negativity occurring between the paired stimuli should be reserved for the frontal iCNV, since the essence of expectancy consists of a stimulus-related preparation oriented to upcoming stimuli but not to motor preparation or response execution, which is probably reflected in the terminal CNV (tCNV) [2,8,19]. In order to decide whether there was substan-