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Prestimulus EEG alpha activity reflects prestimulus top-down processing

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Abstract

In order to test the hypothesis that prestimulus alpha activity reflects top-down inhibitory processing, EEG was recorded from 16 subjects performing a color and a shape discrimination task. Both tasks required the inhibition of the task-irrelevant feature. Longer reaction times and P3 latencies showed that the shape task was more difficult than the color task. We suppose that these different task-difficulties are due to a higher salience of the color feature as compared to the shape feature. Interestingly, we observed significantly higher prestimulus total alpha activity in the shape task than the color task. We concluded that the inhibition of the more salient color feature in the shape task resulted in enhanced prestimulus alpha activity. Such a relationship between prestimulus alpha and poststimulus performance implies that prestimulus alpha reflects prestimulus top-down processing for preparing subsequent task-performance. Since we observed the 'task' effect of prestimulus alpha activity also in reaction times and in P3 latencies, prestimulus alpha seems to predict such poststimulus responses. Consequently, prestimulus ongoing alpha activity probably reflects top-down information and modulates subsequent poststimulus responses.
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It has been reported that there is a substantial relationship between mental (cognitive) states and oscillatory brain activity [4,6,16]. Moreover, it has been suggested that momentary states of the brain, determining the response to a stimulus, may be reflected in the ongoing EEG [3,5,7]. Since brain oscillations in the EEG alpha band (approximately 10 Hz) have been known as the most prominent brain oscillation present during relaxed wakefulness [1,28], spontaneous alpha activity most probably reflects a momentary mental state in relaxed wakefulness. Likewise, we supposed that top-down processing prior to stimulation would be reflected in the prestimulus ongoing alpha activity. In line with this view, we recently observed a significant relationship between prestimulus alpha dominance and P1 amplitude in favor of phase-resetting of ongoing alpha activity (Min et al., unpublished observations). Since the early event-related potentials (ERPs) reflect the early manifestation of interactions between top-down and bottom-up processes [25,33], our findings suggested that the predominant ongoing alpha activity prior to stimulation might serve a certain purpose with respect to poststimulus mental processes. Klimesch et al. [25] recently postulated that alpha synchronization might reflect a top-down function in inhibiting task-irrelevant information, since the event-related synchronization in the alpha band can be noticeably observed during task-performance either under such conditions where subjects have to withhold task-relevant information or over the brain regions that are task-irrelevant [8,11,21,23,24,32,34]. Therefore, by means of two kinds of discrimination tasks requiring inhibition of concurrent task-irrelevant feature processing for improving task-performance, here we would like to test a putative relationship between prestimulus EEG alpha dynamics and poststimulus responses of task-performance from the viewpoint of top-down inhibitory processing.

Sixteen subjects participated in this study (11 females, mean age 24; range 20–31 years). This research was carried out in accordance with local ethics guidelines and the Declaration of Helsinki (World Medical Association: Ethical Principles for Medical Research Involving Human Subjects, 1964). All subjects showed no signs 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).

Two stimuli randomly drawn from a set of red or green circles or squares were presented bilaterally on a light-gray background

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at an eccentricity of 3° visual angle on a computer monitor, which was placed in front of the subject at a distance of 100 cm. Each stimulus spanned 4° visual angle for a duration of 700 ms. Stimulus presentation was followed by a variable inter-stimulus-interval ranging from 1300 to 1700 ms with a mean value of 1500 ms. The areas of circles and squares were matched and all types of stimuli appeared pseudo-randomly with equal probability. Prior to the experiment, we flickered red and green squares on the screen and instructed subjects to adjust the RGB values of the squares until the observed flickering was minimized. The resulting individual isoluminant RGB values for red and green were then used for the experiment.

In the main experiment, subjects were required to remain centrally fixated, and were instructed to press a button with the index finger of one hand if the task-relevant feature ('color' or 'shape' in a 'color task' and a 'shape task', respectively) was the same, and to press a button with the other hand if not (cf. Fig. 1). Since Mordkoff and Yantis [27] reported that coactivation occurs when target attributes from two separable dimensions are simultaneously present, but not when target attributes come from the same dimension, here we employed two dimensions (color and shape) to induce such coactivation, requiring subjects to inhibit the task-irrelevant feature for improving performance. In order to analyze reaction times, subjects were asked to press the button as quickly as possible. Response hands and the sequence of presented tasks were counterbalanced across subjects. Stimuli in each task were presented in four blocks, separated by short rest periods in between.

Stimuli were classified according to whether the task-relevant or task-irrelevant feature (color or shape) of the bilaterally presented stimuli was the same or not. Consequently, we had four categories of stimulus-condition, as illustrated in Fig. 1. The 'identical' condition represented identical features in both color and shape dimensions across bilaterally presented stimuli. In the 'color-only' condition, stimulus pairs were presented with identical colors. On the other hand, in the 'shape-only' condition we presented stimulus pairs with identical shapes. In the 'neither' condition, neither color nor shape were the same across the presented stimuli. The experiment consisted of 100 trials per stimulus-category, resulting in a total number of 400 trials

for each task. Data were averaged within each stimulus-category and only trials with correct responses were further analyzed.

EEG was recorded using a BrainAmp amplifier (Brain Products, Munich) with 32 sintered Ag/AgCl-electrodes mounted in an electrode cap (Easycap, Falk Minow Services, Munich) and placed according to the 10-10 system, with a nose-tip reference and ground electrode at AFz. Eye movement activity was monitored with an electrode placed sub-orbitally to the right eye and was referenced to the nose. Electrode impedances were maintained below 10 kΩ prior to data acquisition. EEG was analogue filtered from 0.016 to 250 Hz, digitized at 500 Hz and stored for off-line analysis. Recordings were made while subjects sat in a sound-attenuated and electrically shielded booth. Data were epoched from 500 ms before to 1000 ms after stimulus onset. Automatic artifact rejection excluded trials from further processing if the standard deviation within a moving 200 ms time interval exceeded 30 μV. Subsequently, all epochs were visually inspected for artifacts, and epochs containing eye-movements or electrode drifts were rejected.

For investigating the amplitude and time-course of oscillatory activity, the EEG signals were convolved with Morlet wavelets [19,20]. The wavelet transform was performed for each individual trial, and the absolute values of the resulting transforms were averaged. This measure reflects the 'total activity' for a certain frequency range, irrespective of whether it is phase-locked to the stimulus or not. Since activity in a prestimulus period would vanish after baseline correction, no baseline correction was applied to the total alpha activity.

It has been demonstrated that subjects differ considerably in their 'individual alpha frequency (IAF)' [12,24]. Therefore, the frequencies used in the wavelet analyses of total alpha activity were determined individually for every subject. Time-frequency transforms for total activity were first computed for the electrode Pz, where the poststimulus amplitude modulation of alpha activity was most pronounced. From this time-frequency scalogram, the IAF was obtained as the maximum of total activity in the frequency range between 8 and 13 Hz in a time window from 400 to 200 ms prior to stimulus onset. For obtaining a single IAF irrespective of stimulus-categories and task-types, we averaged such maxima across all four stimulus-categories and both tasks

Fig. 1. This schematic table shows four sample stimulus pairs representing each stimulus-category. Depending on whether the two features color and shape are identical, all stimuli are classified into 2 × 2 stimulus-categories. The colors green and red used in the experiment are represented in the figure by gray and black, respectively.

Fig. 2. (A) Grand-averaged time courses of total alpha activity at electrode Pz, (B) grand-averaged ERPs at electrode Pz and (C) a bar graph of reaction 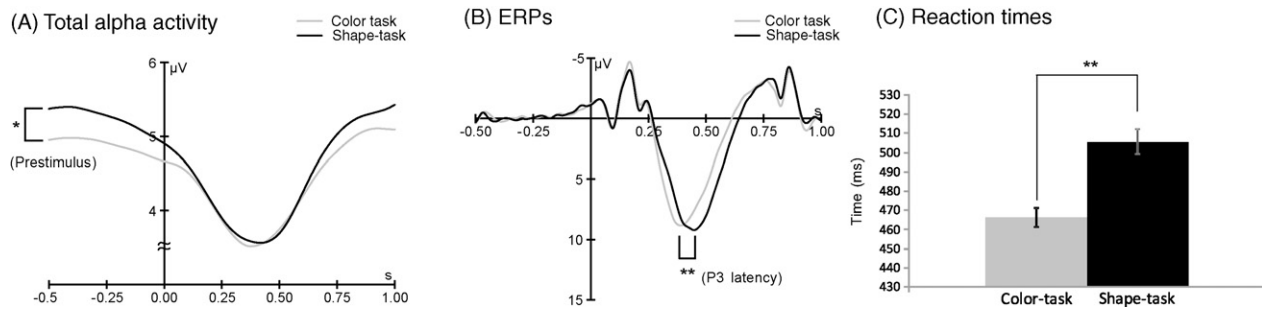times. These data are averaged across four categories of stimulus-condition in both tasks. Gray lines (or a gray bar) indicate the color task and black lines (or a black bar) the shape task. In (C), error bars represent ±1 standard error of the mean. For display of ERPs, we applied a 20 Hz low-pass filter. Notice the significant differences indicated by brackets: prestimulus levels of total alpha activity in (A); P3 latencies in (B); reaction times in (C). The number of asterisks indicates the level of statistical significance: $^{*}p < .01$ and $^{**}p < .0005$.

within each subject. If there was no identifiable alpha peak (i.e. no local maximum) within such a time-frequency range, 10 Hz was selected as the IAF for those subjects. This had to be done for four subjects.

Reaction times were collected within their individual 95% confidence interval. The amplitude and latency of the P3 component were also evaluated. For the P3 analysis, we performed a baseline correction and assessed the maximum amplitude and latency of the P3 within the time window from 300 to 600 ms poststimulus. We analyzed all measures on the electrode Pz where poststimulus effects of both parieto-occipital alpha activity [1] and the P3 component [30] overlap and are most pronounced. In order to obtain the prestimulus total alpha activity, we measured mean values of the total alpha activity in the time window from 400 to 200 ms prestimulus. This time window was chosen to avoid the temporal smearing[1] of poststimulus activity into the baseline [19], and to include a reasonable period having more than one cycle of alpha frequency.

All measures were analyzed with a repeated measures ANOVA comprising two within-subjects factors labeled as 'task' ('color task' versus 'shape task') and 'condition' ('identical' versus 'color-only' versus 'shape-only' versus 'neither') and a between-subjects factor labeled as 'task-order' ('color-first' versus 'shape-first'). We introduced the sequence of presented tasks as a between-subjects factor in order to check whether task-shifting between experimental blocks influences task-performance. The Greenhouse–Geisser correction was used where appropriate. To analyze subjects' experience during the task, a short interview was additionally performed after the experiment.

We observed that the reaction times in the color task were significantly shorter than those of the shape task ($F(1,14) = 44.222$, $p < .0005$; cf. Fig. 2C). There was also a significant 'condition' effect ($F(3,42) = 17.624$, $p < .0005$) and a significant interaction effect on reaction times ('task' × 'condition': $F(3,42) = 14.342$,

$p < .0005$). For the P3 amplitude, we found a strong 'condition' effect ($F(3,42) = 25.157$, $p < .0005$) and a significant interaction effect ('task' × 'condition': $F(3,42) = 8.611$, $p < .0005$), but no significant 'task' effect ($F(1,14) = 2.159$, ns). As for the P3 latency, there were main effects of both 'task' ($F(1,14) = 44.247$, $p < .0005$; cf. Fig. 2B) and 'condition' ($F(3,42) = 9.392$, $p < .0005$). The interaction effect between them also turned out to be significant ($F(3,42) = 10.210$, $p < .0005$).

We found that the shape task was preceded by significantly higher prestimulus total alpha amplitudes than the color task ($F(1,14) = 5.024$, $p < .05$; color task: 4.9 μV; shape task: 5.3 μV; cf. Fig. 2A). In addition, we noted a significant interaction ('task' × 'task-order': $F(1,14) = 6.384$, $p < .05$). No other main effects or interactions yielded significant results.

The shape task yielded significantly longer reaction times and P3 latencies as well as higher amplitudes of *prestimulus* total alpha activity than the color task (cf. Fig. 2). These findings suggest that the prestimulus alpha activity seems to have a functional relationship with reaction time and P3 latency. Since modulation of reaction times and P3 is considered to be indicative of different efficiencies in information processing [13,26,29], our findings indicate that the shape task is more difficult than the color task. As the shape task resulted in longer reaction times than the color task, the color feature seemed more salient than the shape feature. In the shape task, subjects should inhibit perceptual processing of the color feature for improving task-performance, and vice versa in the color task. Presumably, subjects prepared an adequate mental state for inhibition before stimulation. If enhancement of alpha activity reflects a top-down inhibitory control as Klimesch et al. [25] suggested, the higher prestimulus alpha amplitude in the shape task than the color task implies that more inhibition is necessary for performing the shape task in advance of stimulation. That is, suppressing the perceptual processing of the color feature in the shape task requires more prestimulus alpha activity. Since the color feature is more salient than the shape feature, it seems plausible to assume that inhibiting the salient color feature requires more alpha activity prior to stimulation in order to perform the upcoming shape task efficiently. This interpretation of the prestimulus alpha activity is in line with Klimesch's inhibition hypothesis [25].

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[1] Smearing is an artefact by wavelet transformation. The wavelet transformation considers multiple time points around the respective time point for convolution, and thus the peak width of the convolved signal will be smeared even into the baseline. Accordingly, the baseline should be chosen to fairly precede the stimulation.

Other plausible interpretations are also worth considering. For instance, it seems plausible to assume that different arousal levels depending on task-difficulty account for the present results, since alpha activity has been generally reported as being negatively correlated with an individual's arousal [2]. According to this arousal hypothesis, a more difficult task should reveal less prestimulus alpha activity, since increased arousal in preparing a more difficult task may result in a reduction of alpha activity in advance of stimulation. However, we observed that the more difficult task (i.e. the shape task) yielded more alpha activity prior to stimulation, which can hardly be explained by the arousal hypothesis. In this respect, the inhibition hypothesis seems more likely for interpreting the present findings. However, future studies need to investigate this relationship more closely.

A number of studies reported that prestimulus alpha activity modulates poststimulus ERPs [15,17,22]. This indicates that prestimulus alpha activity can influence poststimulus cognitive processing, which we will consider the weak hypothesis about prestimulus alpha activity. Even more interestingly, it has been demonstrated that the alpha phase at stimulus onset or prior to stimulus onset modulates human reaction time [9,10,14,18,31]. This indicates that prestimulus alpha activity even influences human performance, which we will consider the strong hypothesis about prestimulus alpha activity. Our data show that prestimulus alpha activity influences reaction time as well as P3 latency. Since P3 latency is closely related to reaction time [35], our findings support the strong hypothesis about prestimulus alpha activity. In conclusion, our data together with previous findings support the notion that prestimulus alpha activity can influence both poststimulus cognitive processing and even the manual response that results from this processing. Such a prestimulus alpha influence on the poststimulus performance implies that prestimulus alpha activity reflects a top-down preparatory mental state for upcoming task-performance.

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