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Effects of task difficulty on evoked gamma activity and ERPs in a visual discrimination task

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Abstract

Objective: The present study examined oscillatory brain activity of the EEG gamma band and event-related potentials (ERPs) with relation to the difficulty of a visual discrimination task.

Methods: Three tasks with identical stimulus material were performed by 9 healthy subjects. The tasks comprised a passive control task, and an easy and a hard visual discrimination task, requiring discrimination of the color of circles. EEG was recorded from 26 electrodes. A wavelet transform based on Morlet wavelets was employed for the analysis of gamma activity.

Results: Evoked EEG gamma activity was enhanced by both discrimination tasks as compared to the passive control task. Within the two discrimination tasks, the latency of the evoked gamma peak was delayed for the harder task. Higher amplitudes of the ERP components N170 and P300 were found in both discrimination tasks as compared to the passive task. The N2b, which showed a maximum activation at about 260 ms, was increased in the hard discrimination task as compared to the easy discrimination task.

Conclusions: Our results indicate that early evoked gamma activity and N2b are related to the difficulty of visual discrimination processes. A delayed gamma activity in the hard task indicated a longer duration of stimulus processing, whereas the amplitude of the N2b directly indicates the level of task difficulty. © 2002 Elsevier Science Ireland Ltd. All rights reserved.

Keywords: Event-related potential; P3; Gamma; 40 Hz; Difficulty; Color discrimination

1. Introduction

The EEG gamma band (range about 20–80 Hz) has been reported to be closely related to binding processes (Engel and Singer, 2001; Tallon et al., 1995), priming effects (Elliott et al., 2000), affective processing (Keil et al., 2001; Müller et al., 1999), visual attention (Fries et al., 2001; Müller et al., 2000) and memory processing (Fell et al., 2001; Herrmann and Mecklinger, 2001; Tallon-Baudry et al., 1998). One aspect which has not yet been examined is the relation between EEG gamma activity and task difficulty. Some evidence for a relation between EEG gamma activity and task difficulty came from studies which compared EEG gamma activity for target and non-target stimuli in visual discrimination tasks. Evoked gamma activity in visual discrimination tasks was found to be higher in targets than in non-targets (Herrmann et al., 1999; Herr-

mann and Mecklinger, 2000). Longer reaction times (RTs) and higher error rates for targets as compared to non-targets indicate that targets are more difficult to discriminate than non-targets. However, targets in previous experiments were compared with non-targets. Therefore, the increased gamma activity could also have been related to the infrequent response to the target stimulus. Further evidence for a relation between gamma activity and difficulty resulted from memory tasks which showed that EEG gamma activity is positively related to memory load (De Pascalis and Ray, 1998). So far no study has explicitly examined the relation between difficulty in visual discrimination processes and EEG gamma activity.

The relation between event-related potentials (ERPs) and task difficulty has been investigated in various studies. Task difficulty has been mainly associated with the ERP components N1, N2 and P3. With regard to the latency of the N1 in visual discrimination tasks we will refer to the N1 component as N170. Ritter et al. (1982, 1988) found an increased negative deflection in the time interval of the N170 and N2 component in a choice-RT task as compared to simple-RT tasks. The N2 has also been associated with discrimination processes (Breton et al., 1988; Ritter et al., 1983). Smid et

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al. (1999) compared the latencies of the posterior N2 component (N2b) in an easy and a hard color discrimination task. The latency of the N2b was delayed when color was hard to discriminate compared with when it was easy to discriminate. The N2b, which has its maximum over the vertex (Näätänen et al., 1978), seems to be a marker of the intensity of discrimination processes. Another ERP component which has been associated with discrimination tasks is the P3 (Mecklinger et al., 1998). Most studies which investigated the visual or auditory evoked P3 found a delay of latency and a decrease of amplitude for more difficult discrimination processes, especially when comparing target stimuli with non-target stimuli (Polich, 1987; Palmer et al., 1994; Hoffman et al., 1985). The P3 latency and amplitude effects were found at frontal and posterior electrode sites (Comerchero and Polich, 1999).

In the present study we examined ERPs and EEG gamma activity in 3 tasks with different levels of difficulty. In all tasks the identical color stimuli were used as stimulus material. Gamma activity and ERPs of the same non-target stimulus were compared between all tasks. By comparing the same stimulus over all tasks we controlled for the influence of different factors which are related to EEG gamma activity, such as motor responses (Crone et al., 1998) and differences in the processing of different colors (Krüger et al., 2002). Possible differences in EEG gamma activity and ERPs are therefore mainly attributable to the difficulty of the visual discrimination task.

2. Methods

The experiment consists of 3 different tasks. All tasks employed a red circle and two green circles as stimulus material. Even though the luminances of all colors were equal, we will refer to the two green stimuli as 'light green' and 'dark green' to differentiate them verbally. The circles were presented 100 times each, in random order. In the first task (passive task) subjects were instructed to keep their eyes still and watch the stimuli without any task. An easy and a hard discrimination task followed the passive task. The order of the two discrimination tasks was randomized across subjects. In the easy task subjects were instructed to respond with a button press of their right thumb to the red circle and with a button press of their left thumb to both green circles. In the hard task subjects were instructed to respond with a button press of their right thumb to the light green circle and with a button press of their left thumb to the other two circles. In contrast to the easy task, subjects had to discriminate the two similar green circles in the hard task. RTs and EEG data were recorded during the tasks. The focus of the EEG and wavelet analysis was the comparison of the dark green circle across all 3 tasks since it served as non-target in all tasks. The response requirements and frequency of this stimulus were equal in both discrimination tasks.

2.1. Subjects

Fifteen subjects (age 23.4 ± 2.0 years, 8 female) participated in the experiment. Six of the subjects had to be rejected from the analysis because their EEG data failed our criterion of at least 50 valid trials for each condition (see below). The remaining 9 subjects (age 23.4 ± 1.7 years, 6 female) were included in the data analysis. All subjects were right-handed and had normal or corrected-to-normal vision. They showed no signs of neurological or psychiatric disorder and all gave written informed consent to participate in the study.

2.2. Stimuli

Three circles with different colors were used as stimulus material. Circles were presented separately. The size of the circles was 6.5° of visual angle. All circles had a luminance of about 4.5 cd/m^2 and were presented on a white background with a luminance of about 53 cd/m^2. According to the Commission International d'Eclairage (CIE) the colors had the following X, Y coordinates: red ($X = 0.584$, $Y = 0.345$), light green ($X = 0.291$, $Y = 0.536$) and dark green ($X = 0.257$, $Y = 0.468$). CIE coordinates and luminances were measured with a Minolta Chroma Meter CS-100. Stimuli were presented for 800 ms with randomized inter-stimulus intervals ranging from 1150 to 1350 ms. In the two discrimination tasks a feedback 'right' or 'wrong' was presented for 400 ms at the center of the screen succeeding each trial.

2.3. Data acquisition

The EEG was recorded with NeuroScan amplifiers using 26 tin electrodes mounted in an elastic cap. Electrodes were placed according to the International 10–10 system. The ground and reference electrode were placed near the left mastoid (M1). Electrode impedance was kept below 5 kΩ. Horizontal and vertical electrooculogram (EOG) recordings were registered with 4 additional electrodes. Data were sampled at 500 Hz and analog-filtered with a 0.05 Hz high-pass and a 100 Hz low-pass filter. Data were further filtered with a digital 0.5 Hz high-pass filter before analyzing. An additional digital 20 Hz low-pass filter was applied before displaying the ERP data. Averaging epochs for ERP and EEG gamma activity lasted from 100 ms before to 800 ms after stimulus onset. For artifact suppression, trials were automatically excluded from averaging, if the standard deviation within a moving 200 ms time interval exceeded 30 μV in any one of the channels. After the automatic artifact rejection all trials were visually inspected and rejected if eye movement artifacts or electrode drifts were visible. We set a criterion of at least 50 valid trials per condition for data analysis.

2.4. Data analysis

Selected electrode sites were pooled to 4 topographical regions of interest (ROIs) to avoid a loss of statistical power that is inherent when repeated measures ANOVAs are used to quantify multi-channel EEG data. The left anterior region (LAR) was comprised of electrodes FP1, FC3, F3 and F7 while the left posterior region (LPR) included electrodes P3, O1, CP5 and P7. Regions over the right hemisphere included the homologous electrodes. For statistical analyses, ERP amplitudes were pooled across the electrodes in each of the ROIs. Fig. 4 shows ERPs of the standard dark green circle in the 3 tasks. In all tasks, a N170 was evoked around 170 ms after stimulus onset. In the two discrimination tasks an additional posteriorly pronounced negative ERP deflection at about 260 ms was evoked, the so called N2b component. Targets in both discrimination tasks also evoked a target P3. Latencies of P3 were about 350 ms in the easy and 550 ms in the hard task (see Fig. 5). For data analysis we defined ERP components as mean amplitudes in the following time intervals: 150–190 ms (N170), 240–280 ms (N2b), 300–500 ms (early P3) and 500–700 ms (late P3). For the dark green stimulus, which served as standard in all 3 tasks, ANOVAs were computed for these time inter-

vals comprising factors task and ROI. A further ANOVA investigated differences between the two target stimuli for the two discrimination tasks.

For the interpretation of gamma activity it is important to distinguish whether the oscillations occur phase-locked to a stimulus (evoked activity) or with variable phase relative to a stimulus (induced activity). For the analysis of gamma activity, a wavelet transform based on Morlet wavelets was employed. The details of the wavelet transform have been explicitly described in a previous article (Herrmann et al., 1999). According to Galambos (1992), at least 3 types of gamma activity can be differentiated: 'spontaneous', 'induced' and 'evoked'. The 'spontaneous' gamma activity is completely uncorrelated with the experimental setting. This activity is probably due to neuronal processes that do not relate to the task at hand. 'Spontaneous' gamma activity usually cancels out completely if an average ERP is computed across enough trial repetitions. For this reason, we do not focus the EEG gamma analysis on this type of activity. In contrast to the 'spontaneous' gamma activity, the 'induced' and 'evoked' gamma activity are related to the onset of an experimental condition. Fig. 1 shows the differences between induced and evoked gamma activity.

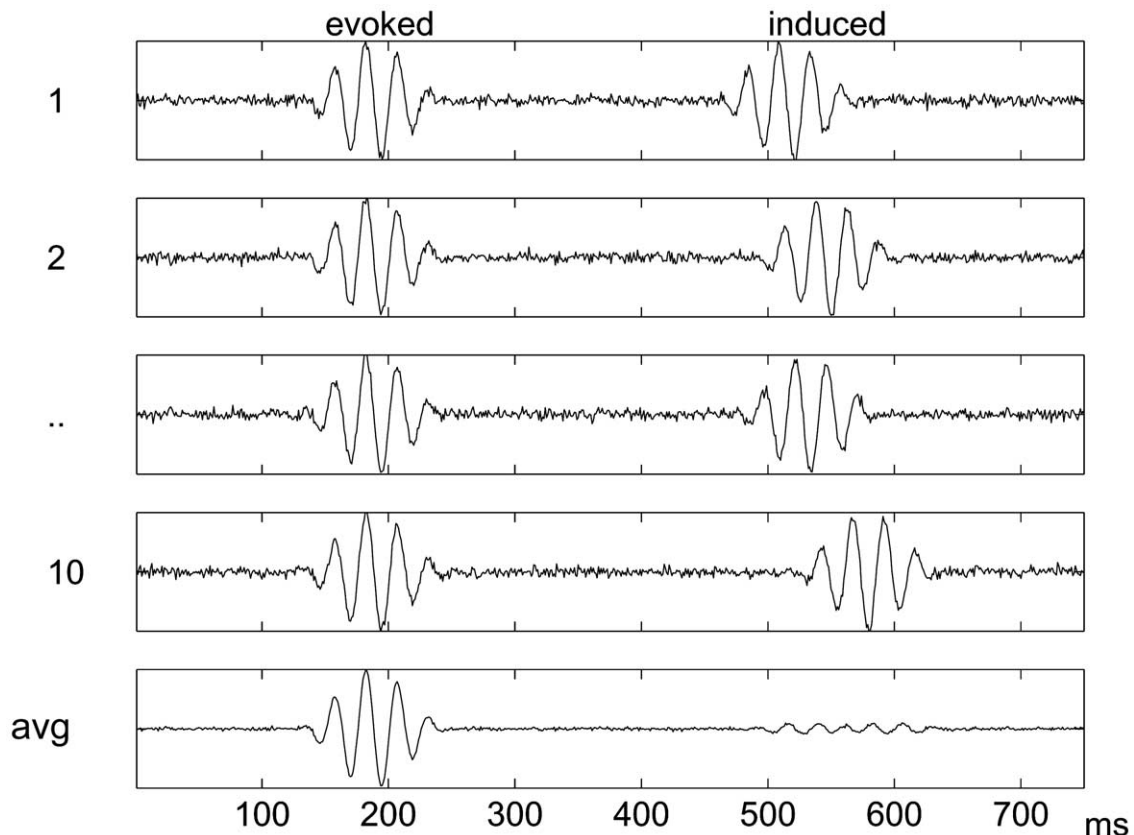To differentiate between evoked and induced activity,

Fig. 1. Oscillations which occur at the same latency after stimulus onset with the same phase relative to stimulus onset in multiple trials (rows 1–4) are considered evoked by the stimulus (left). Evoked activity appears in the average (bottom row). Oscillations with latency or phase jitter relative to stimulus onset (right) are considered to be induced by the stimulus. Induced oscillations are cancelled out in the average. From Herrmann and Knight (2001, p. 471), with permission of the authors.

each subject's ERP was transformed to yield evoked gamma activity and averages of transforms of single epochs were computed to yield induced activity. The frequency of gamma activity used for the wavelet analysis was individually adapted via the time-frequency plane of the O1 and O2 electrodes (Fig. 2) in response to the red circle in the easy task. The individual gamma activity was defined as the highest activation in a frequency range of about 20–80 Hz in a time range of about 60–200 ms. Using this definition the individually adapted gamma activity ranged from 25 to 45 Hz. In analogy to previous studies of Herrmann and Mecklinger (2001) we analyzed gamma band activity evoked by the dark green standard stimulus in an early (60–120 ms) and in a late time interval (150–250 ms) by means of an ANOVA using the same factors as for the ERP data. A further ANOVA investigated the differences between the two target stimuli. In order to examine the relations between the latencies of the EEG gamma activity and the P3 component of the ERPs we calculated a Pearson correlation coefficient.

3. Results

3.1. Behavioral data

Mean RTs and error rates of the easy and the hard discrimination task are shown in Fig. 3. A comparison of RTs between the standard dark green stimulus in the hard (570 ms) and the easy (408 ms) task yielded longer RTs in the hard task ($F(1, 8) = 78.9, P < 0.0001$). The same effect was found for the targets in the two tasks. RTs of the target circle (light green) in the hard task (614 ms) were significantly longer as compared to the target circle (red) in the easy task

(428 ms; $F(1, 8) = 117, P < 0.0001$). The delay of RTs in the hard task indicates longer stimulus processing.

At the next step the error rate of the two discrimination tasks was analyzed. Thereby, a higher error rate was found in the hard (8.8%) as compared to the easy task (2.0%). Comparing the error rate of the standard circle (dark green) in the two tasks yielded a significantly higher error rate in the hard (9.8%) as compared to the easy task (1.1%; $F(1, 8) = 17.50, P < 0.005$). A higher error rate was also found for the target in the hard (15.0%) as compared to the target in the easy task (3.3%; $F(1, 8) = 22.72, P < 0.005$).

Longer RTs and higher error rates indicated that the hard task was in fact harder to perform than the easy task.

3.2. ERP responses

An ANOVA of N170 amplitudes in response to the standard dark green circle yielded a significant main effect of task ($F(2, 16) = 10.25, P < 0.005$), indicating larger amplitudes for the easy (-1.51 μV) and the hard (-1.78 μV) discrimination tasks as compared to the passive task (0.02 μV; Fig. 4). A significant task × ROI interaction revealed that this effect is pronounced at posterior ROIs ($F(6, 48) = 3.82, P < 0.05$). Post-hoc comparisons showed no differences between the dark green circle in the easy and in the hard task ($F(1, 8) = 0.35, P < 0.6$). However, compared with the control condition higher N170 amplitudes were found for the easy ($F(1, 8) = 10.89, P < 0.05$) and the hard task ($F(1, 8) = 24.84, P < 0.005$), indicating that the N170 has a generally higher amplitude when performing a discrimination task, but is not associated with the level of difficulty. Amplitudes in the time interval of the N2b also differed between the 3 tasks ($F(2, 16) = 5.06, P < 0.05$). Furthermore, a significant
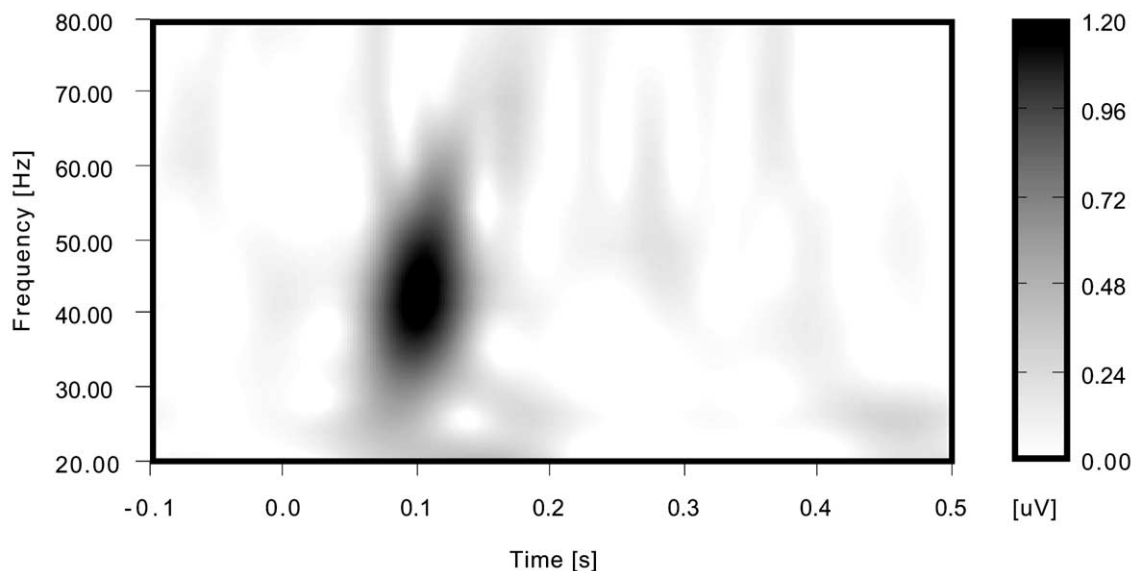

Fig. 2. Time-frequency plane of the electrode 'O2' (in one subject). After 100 ms an early peak of gamma activity was evoked at a frequency of about 43 Hz.
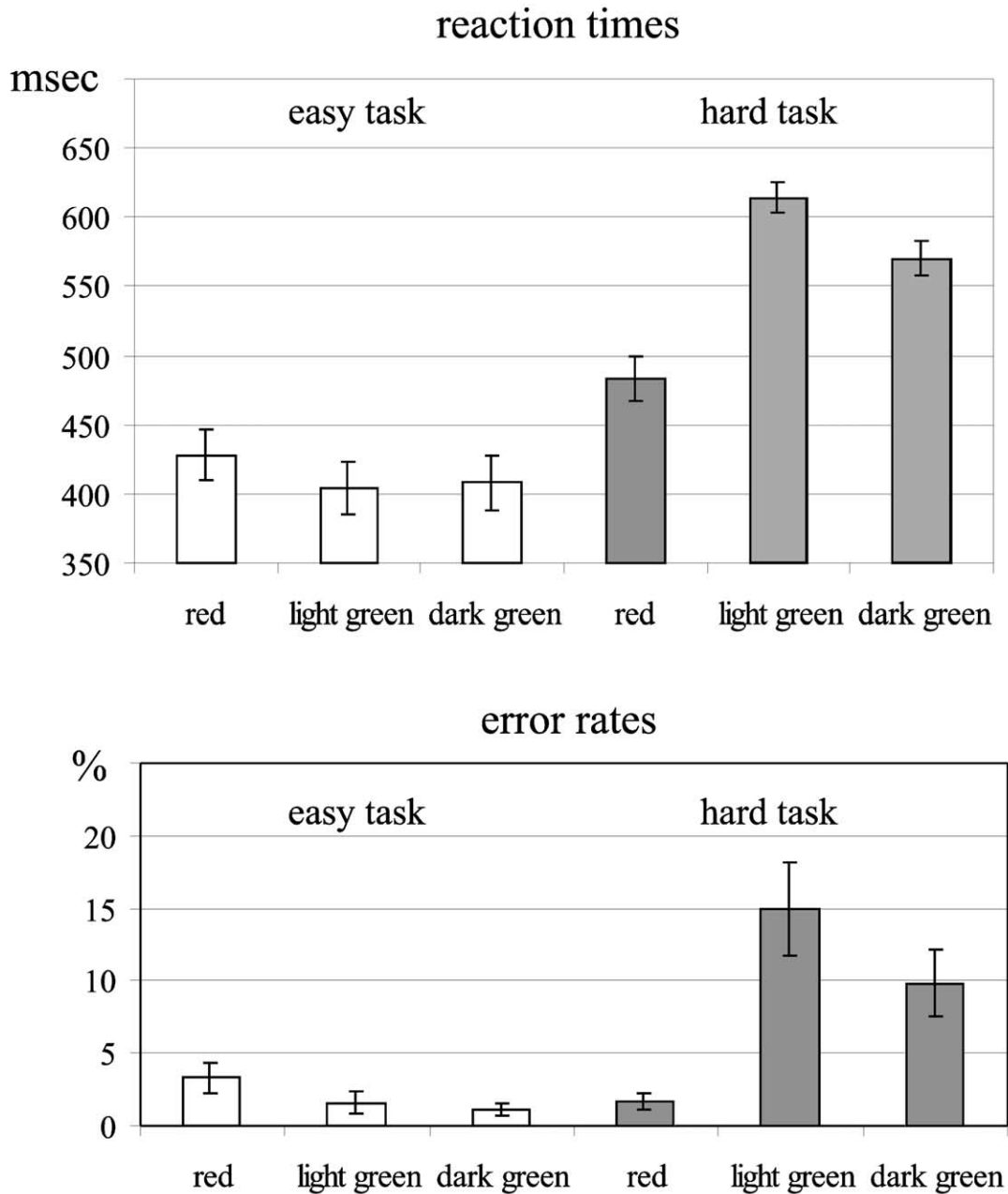
reaction times

error rates

Fig. 3. Mean RTs and error rates in the easy and hard discrimination tasks. The upper figure shows RTs with standard error of the mean. The lower figure shows error rates with standard error of the mean. Notice higher error rates and longer RTs for the target stimulus (red circle in the easy task, light green circle in the hard task) and dark green standard stimulus in the hard task.

task $\times$ ROI interaction was found for N2b amplitudes ($F(6, 48) = 5.04$, $P < 0.05$), indicating that N2b effects were pronounced at posterior ROIs. A post-hoc comparison for anterior and posterior regions of the easy and the hard task revealed a significantly enhanced N2b amplitude in the hard task for posterior regions ($F(1, 8) = 15.65, P < 0.005$) but not for anterior regions ($F(1, 8) = 0.03$, $P < 0.9$). Amplitude differences of the standard dark green circle were also found in the time interval of the early P3 ($F(2, 16) = 9.49, P < 0.005$). As for the N2b, a significant task $\times$ ROI interaction was found ($F(3, 24) = 6.45$,

$P < 0.05$). This interaction emerges due to the fact that only posterior P3 amplitudes were enhanced in the easy (2.69 µV) as compared to the hard task (1.25 µV; $F(1, 8) = 10.71, P < 0.05$), whereas no differences between the anterior P3 amplitudes were found ($F(1, 8) = 0.82$, $P < 0.4$). For the time interval of the late P3 component no significant differences were observed for the standard dark green circle between the 3 tasks ($F(2, 16) = 2.81$, $P < 0.1$).

A comparison of the target P3 for the early P3 interval between the easy and the hard task (Fig. 5) revealed
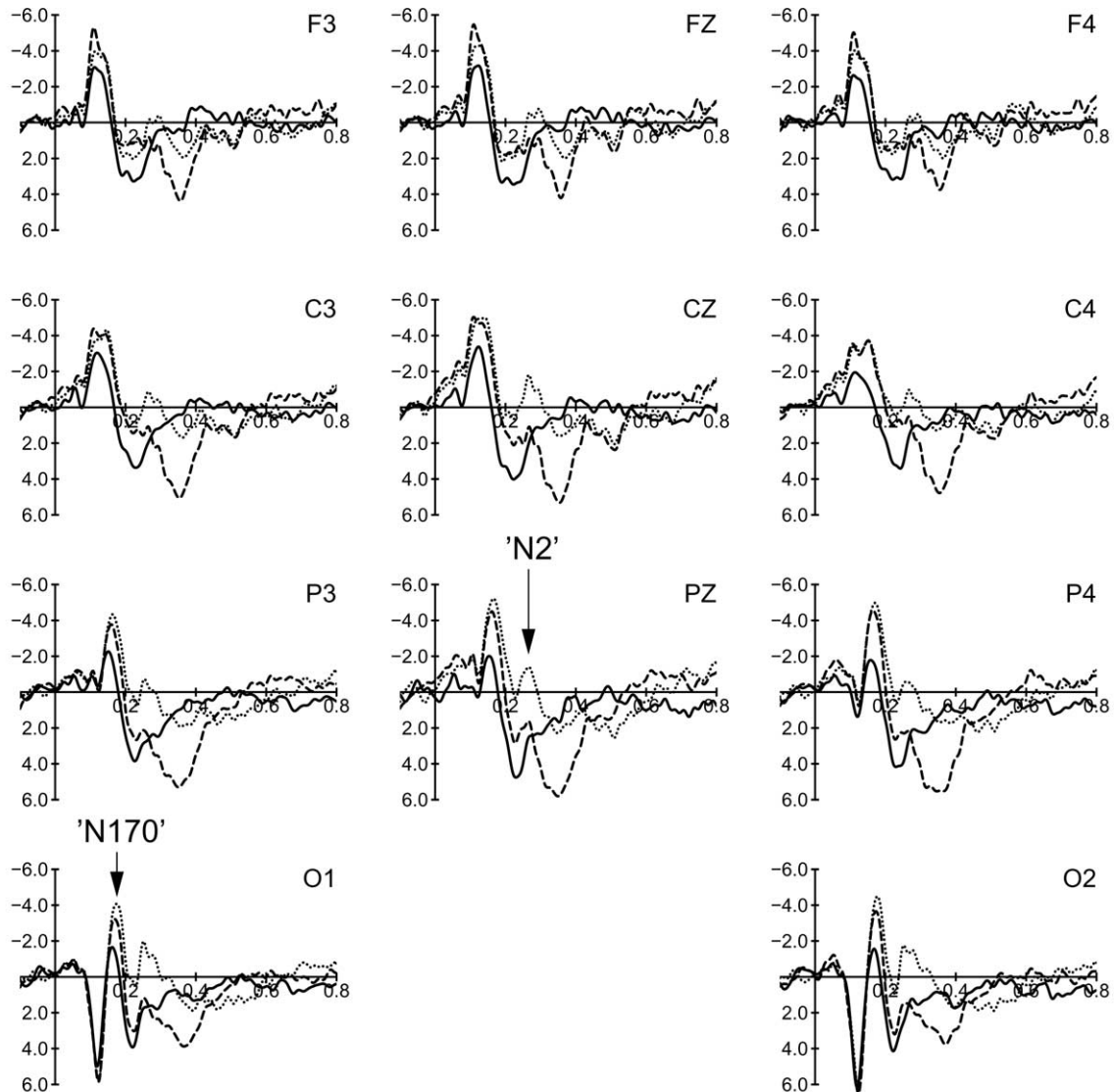
Fig. 4. ERPs averaged across 9 subjects in response to the dark green standard stimulus in the control task (solid), easy task (dashed) and hard task (dotted).

higher amplitudes for the easy (0.93 μV) as compared to the hard task (-0.19 μV; $F(1, 8) = 21.39$, $P < 0.005$). Furthermore, a significant task × ROI interaction ($F(3, 24) = 11.52$, $P < 0.005$) indicates that this effect was strongest at posterior sides. Post-hoc comparisons between anterior and posterior regions showed higher posterior P3 amplitudes in the easy (3.40 μV) as compared to the hard task (0.75 μV; $F(1, 8) = 10.75$, $P < 0.05$). No differences were found for anterior regions ($F(1, 8) = 0.23$, $P < 0.7$). An ANOVA for the target P3 in a later time interval showed higher amplitudes for the difficult (0.92 μV) as compared to the easy task (-0.21 μV; $F(3, 24) = 20.61$, $P < 0.005$). A significant task × ROI interaction ($F(3, 24) = 6.45$, $P < 0.005$) further indicates that this effect was pronounced at posterior sites. Post-hoc analyses revealed enhanced late target P3 amplitudes for the hard task in anterior ($F(1, 8) = 9.31$, $P < 0.05$) and poster-

ior regions ($F(1, 8) = 17.58$, $P < 0.005$). As for the P3, a significant task × ROI interaction was found for the N2b amplitudes of the targets ($F(3, 24) = 6.60$, $P < 0.05$). However, no significant differences were found between the hard and the easy task for anterior ($F(1, 8) = 1.17$, $P < 0.4$) and posterior ($F(1, 8) = 2.39$, $P < 0.2$) regions, indicating that N2b in targets was not enhanced in the hard task. No differences between the target amplitudes were found for the N170 ($F(1, 8) = 1.66$, $P < 0.3$).

3.3. Gamma responses

Bursts of gamma activity after stimulus onset were only found for the evoked EEG gamma activity. The induced gamma activity did not increase after stimulus onset.

Evoked gamma activity at some selected electrodes is shown in Fig. 6 for the standard dark green circles. In all
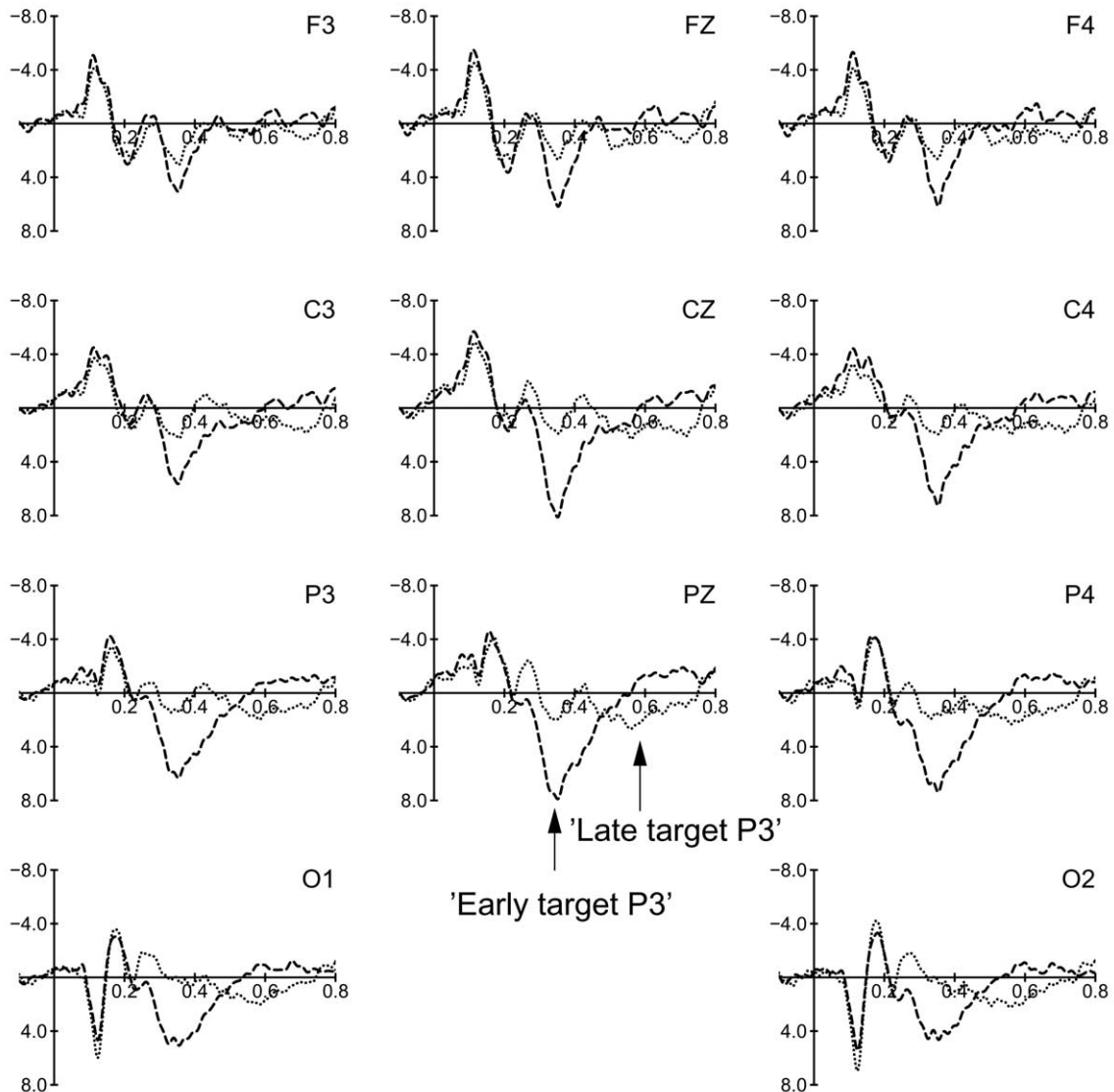
Fig. 5. ERPs averaged across 9 subjects in response to the light green target stimulus in the hard task (dotted) and target red stimulus in the easy task (dashed).

3 tasks a peak of gamma activity was found in a post-stimulus time interval between 60 and 100 ms. An ANOVA for this time interval revealed a significant main effect of task $(F(2, 16) = 4.77, \quad P < 0.05)$. Post-hoc comparisons revealed that the gamma activity for the dark green circle in the easy task (0.34 μV) was larger than the gamma activity in the hard task (0.28 μV; $F(1, 8) = 7.13$, $P < 0.05$) and larger than the gamma activity in the passive task (0.24 μV; $F(1, 8) = 11.17$, $P < 0.05$). A significant task × ROI interaction indicated that these differences were most pronounced over posterior electrodes $(F(3, 24) = 4.33,$ $P < 0.05)$. No gamma differences were found between the hard and the passive task in this time interval.

A second peak of gamma activity was found in the time interval between 150 and 250 ms. An ANOVA for this time interval revealed a significant main effect of task $(F(2, 16) = 9.12, P < 0.005)$. Largest amplitudes for this

time interval were found for the hard task (0.29 μV). Post-hoc comparisons revealed that the amplitudes for the hard task were larger as compared to the amplitudes for the easy task (0.23 μV; $F(1, 8) = 5.58$, $P < 0.05$). Furthermore, post-hoc tests also revealed larger amplitudes for the easy as compared to the passive task (0.17 μV; $F(1, 8) = 6.38$, $P < 0.05$). The ANOVA for the target stimuli revealed no significant differences in evoked gamma activity.

3.4. Latency of evoked gamma responses and P3 amplitudes

For the examination of the relation between evoked gamma activity and P3 amplitude we correlated the latency differences of the posterior Pz electrode between the hard and the easy task for the EEG gamma activity (highest activity in a time range between 60 and 300 ms) with the
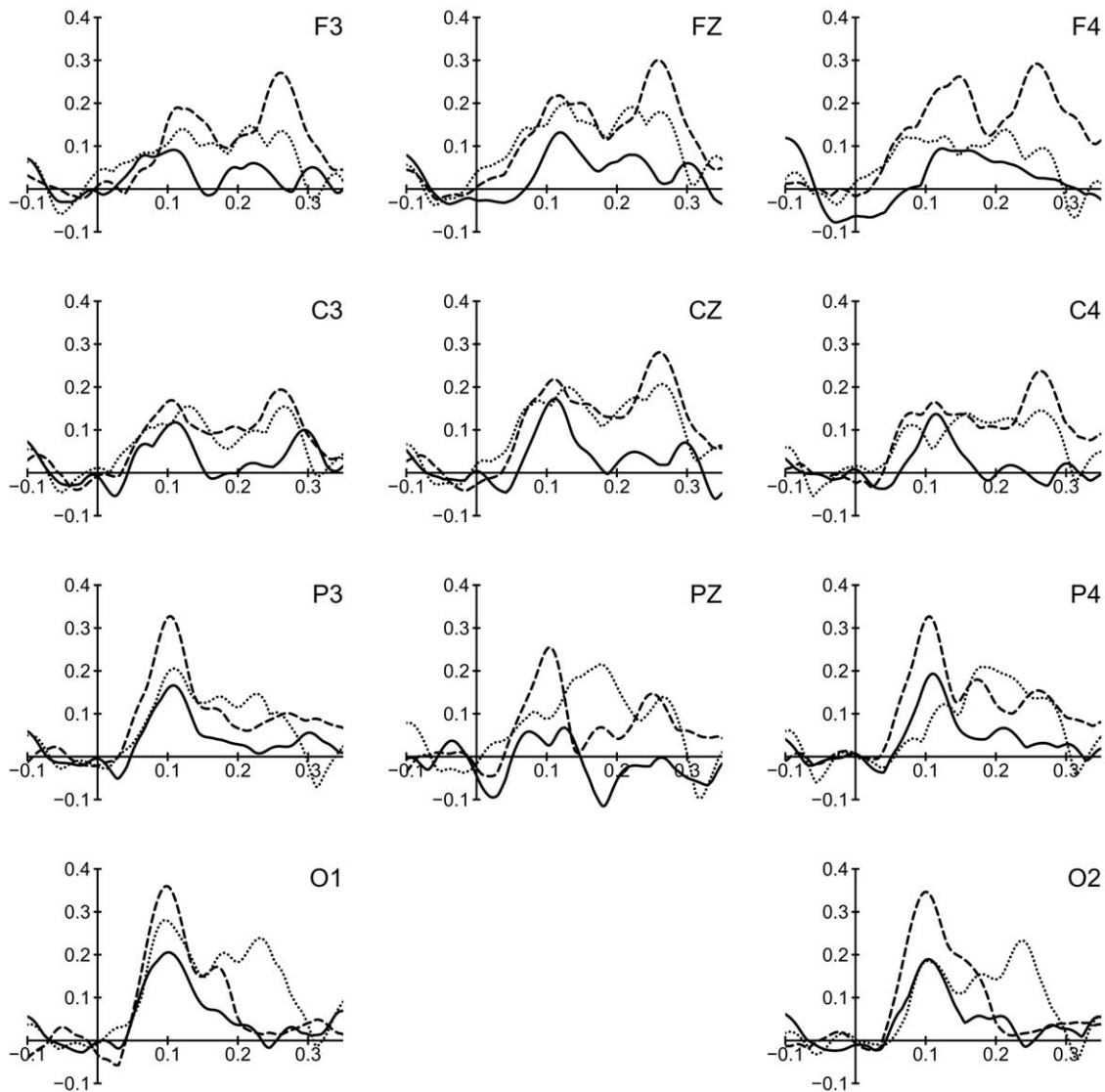
Fig. 6. Evoked EEG gamma activity averaged across 9 subjects in response to the standard dark green stimulus in the control task (solid), easy task (dashed) and hard task (dotted). Notice the second peak of gamma activity in the hard task at about 200–250 ms at posterior electrodes.

latency differences of the P3 component (highest activity in a time range between 300 and 700 ms). In this analysis, a high ($r = 0.53$, $P < 0.15$) but non-significant correlation was found. However, the lack of correlation may be explained by the small number of subjects ($n = 9$) which were included in the calculation of the correlation.

4. Discussion

4.1. Behavioral data

Higher error rates and longer RTs in the hard as compared to the easy task indicated that the hard task was in fact more difficult to perform than the easy task (Fig. 3). Longest RTs and highest error rates in both discrimination tasks were found for the target stimuli. This effect has also been

reported in previous experiments (Teichner and Krebs, 1974; Herrmann and Mecklinger, 2000). A higher error rate and longer RTs for the standard dark green stimulus in the hard task further demonstrated the effect of task difficulty. Longer RTs for the dark green stimulus and the target stimulus additionally indicated a longer duration of stimulus processing in the hard task.

4.2. ERP responses

Our results replicated previous examinations, which found a positive relation between specific ERP components and task difficulty. Most sensitive to task difficulty was the posterior N2b. The N2b component, which has its maximum amplitude at electrode Cz at about 260 ms, was associated with attention to color and target detection effects (Ruijter et al., 2000; Potts and Tucker, 2001). Eimer (1996) examined

two visual discrimination tasks with colored stimuli, where he presented targets among various distractors. He found an enhanced negativity in the time range of the N2 for the target, which he interpreted as a neuronal correlate of an attentional filtering process. Following this interpretation, we propose that the enhanced N2b in the hard task is a marker of the demands of a visual discrimination task. In the present study the demands differ between the two tasks. In the hard task subjects had to perform a color discrimination within one color category (light vs. dark green) and further had to produce the same response to two non-target stimuli (light green and red circle) belonging to two different categories. In particular, the discrimination within the same color category (light vs. dark green) makes the hard task more difficult than the easy task, in which a response can be made based simply on differentiating two major color categories (green and red).

Another component which was associated with task difficulty was the N170. A study which observed timing of color-based attentional processes indicates that this component was probably generated in inferior occipito-temporal cortex (Anllo-Vento et al., 1998). Vogel and Luck (2000) reported an enhanced negative deflection of the N170 component in choice-RT tasks with colorful letter arrays. In their study the influence of task difficulty by varying the distractor colors has been investigated in an easy and in a hard choice-RT task. The target in both tasks was a non-specific red letter. Colors of the distractor letters could either be blue, gray, green or violet (easy task), or shades of purple and pink (hard task). Compared to the simple-RT task, the N170 was increased in both choice-RT tasks. No differences in the time range of the N170 component were found between the easy and hard task. The present study replicated this finding, which indicates that N170 is generally enhanced in visual discrimination processes.

Amplitude differences in the study of Vogel and Luck (2000) were also observed for the time interval of the P3 component. It was suggested that more difficult discriminations tend to produce smaller and later P3s (Polich and Bondurant, 1997; Grillon et al., 1990). In the present study, P3 was also delayed in the hard task as compared to the easy task (Fig. 5). This effect was primarily found at posterior electrodes, which is in line with previous ERP findings (Mangun et al., 1998; Karayanidis and Michie, 1997). The observed delay of P3 amplitude could indicate a longer duration of stimulus evaluation (Donchin and Coles, 1988). This assumption was supported by higher RTs in the hard task.

4.3. Gamma responses

The main purpose of this study was to investigate the relation between the difficulty of visual discrimination tasks and EEG gamma activity. A higher evoked EEG gamma activity was found in two color discrimination tasks as compared to a passive control task. Evoked

gamma activity in an easy discrimination task was found in a time range of about 100 ms. In a hard discrimination task, evoked gamma activity was found in a later time range of about 200 ms. The delay of gamma activity suggests a longer duration of stimulus processing in the hard discrimination task. This interpretation fits well with the assumption of a relation between EEG gamma activity and the processing demands of a task (Simos et al., 2002; Yordanova et al., 1997b). Simos et al. (2002) examined the influence of task complexity on EEG gamma activity by manipulating the complexity of a target stimulus which had to be detected. In an easy task, subjects had to decide whether they saw a specific animal (a dog or a cat) after the presentation of different animal pictures. In more complex tasks, subjects had to detect a stimulus with specific features (e.g. a 4-legged animal among the animal pictures). The authors reported a linear increase in absolute power in the gamma band over right temporoparietal, left occipital, and left frontal regions with increasing task complexity. These regions also showed a relation with task difficulty in the present study, where strongest gamma effects were found at posterior sites (Fig. 6). Posterior gamma activity has been associated with attentional processes in selective visual attention (Fries et al., 2001), in a paired stimuli paradigm (Shibata et al., 1999a) and in target detection (Herrmann et al., 1999). Clinical studies (Miceli et al., 2001; Schoppig et al., 1999), PET examinations (Gulyas and Roland, 1991), fMRI studies (Engel et al., 1997) and animal studies (Hanazawa et al., 2000; Johnson et al., 2001) further showed that different posterior regions like visual cortex, inferior temporal lobe and left superior parietal cortex are crucially involved in visual discrimination processes. We therefore suggest that the delayed posterior gamma activity is related to such discrimination processes.

The finding that only the evoked but not the induced gamma activity was related to the onset of an experimental condition goes well in line with our previous EEG and MEG examinations in visual discrimination tasks (Herrmann et al., 1999; Herrmann and Mecklinger, 2000). In these studies, we also failed to find induced gamma activity related to the experimental conditions. However, an enhanced induced gamma activity has been found in cognitive processes like visual short-term memory (Tallon-Baudry et al., 1998) and learning processes (Gruber et al., 2001). Yordanova et al. (1997a) and Fell et al. (1997) reported a higher degree of phase-locking to targets than to standard stimuli, indicating that task difficulty may alter gamma phase-locking. This may be the reason why we found only evoked but no induced gamma responses: since both color discrimination tasks are at least as hard as a simple target discrimination task, both lead to phase-locked gamma responses.

4.4. General discussion

When interpreting the results with relation to task diffi-

culty one has to keep in mind that the easy and the hard task require different kinds of processing. In the easy task, subjects had to perform a simple color category comparison between the target red and the two non-target green circles. Similar RTs and error rates (Fig. 3) indicate that the two standard stimuli (light and dark green circles) were both processed in a similar way in the easy task. This result contrasts with that found for the hard task, where higher RTs and a higher error rate were found for the dark green circle as compared to the red circle. To execute the hard task, a comparison of two color categories is required. For the detection of the light green circle subjects had to perform a discrimination within the same color category (light green vs. dark green). This discrimination makes the task more difficult to perform. In addition to discrimination within one color category the same response to different color categories (red and green) has to be executed for the two non-target stimuli. This raises the following question: which differences on the behavioral side are most relevant in explaining the presented data?

One factor which might be related to the EEG gamma effects is the different RT of the easy (408 ms) and the hard task (570 ms). Could the delayed motor responses in the hard task be an explanation for the delayed EEG gamma activity? Crone et al. (1998) examined event-related synchronization for the gamma band of the sensorimotor cortex with subdural electrocorticographic electrodes. They found that gamma synchronization began slightly before or during the motor response. The gamma effects (60–250 ms) in the present study were found long before the motor response of the subjects. It is therefore unlikely that different latencies of the motor responses could explain these effects.

Another aspect which might explain the delayed gamma activity in the hard task is a possible inhibition of a target response in the hard task. The two green circles had a very similar color and were therefore difficult to discriminate. For this reason, we propose that the processing of the non-target green stimulus in the hard task requires an inhibition of a target response. Longer RTs and a higher error rate in the hard task for the non-target dark green stimulus as compared to the non-target red stimulus may be indicative of this inhibition of the target response.

The inhibition of a target response has been examined extensively in the go/nogo paradigm where a target response has to be suppressed (Pfefferbaum et al., 1985). In go/nogo studies, an enhanced frontocentral N2 can be observed for the nogo trials (Bokura et al., 2001; Jackson et al., 1999). In the present study the N2 for the non-target dark green stimulus was also enhanced in the hard task as compared to the easy task in frontal regions. This could indicate the inhibition of a target response for the non-target green stimulus. However, the strongest N2 differences were found at posterior sites and not at frontal sites (Fig. 4), indicating that the enhanced posterior N2 in the hard task is directly related to the difficulty of visual discrimination tasks. Inhibition of

behavior has also been related to the relation to EEG gamma activity (Shibata et al., 1999b). In that study, an enhanced gamma band oscillation was found in central regions (C3, C4 and Cz) in a time range at around 230 ms. Interestingly, this is the same time range where an enhanced gamma activity for the hard task was found (Fig. 6), indicating that the enhanced gamma activity in the hard task might be explained by an inhibition of a target response. However, since target inhibition processes have been primarily related to anterior regions, we argue that these processes cannot explain the posterior gamma effects. We therefore concluded that the delayed posterior evoked gamma activity indicates a longer duration of the discrimination process due to the additional complexity of the hard task (stimulus discrimination within one color category and response discrimination across color categories).

Interestingly, gamma activity reveals the difference in task difficulty within 100 ms whereas ERPs only reflect this difference after about 260 ms. We therefore propose that oscillatory EEG activity may be a better indicator of task difficulty than ERPs are. There are remarkable similarities between evoked gamma activity and ERP data with respect to task difficulty. Evoked gamma activity of the standard dark green stimulus showed a delay of about 100 ms in the hard task (Fig. 6). This delay of gamma activity was similar to the delayed latency of the P3 component in ERPs (Fig. 5). We suggest that the delayed P3 and evoked gamma activity both reflect a longer duration of stimulus processing. This would indicate a close functional relation between evoked gamma activity and the P3 component. A high but non-significant correlation between the latency differences (hard task vs. easy task) of the P3 amplitude and evoked gamma activity is consistent with this conclusion. The assumption of a close relation between oscillatory processes and ERP components was also strongly supported by recently published data (Başar et al., 2001; Makeig et al., 2002). However, further investigations are necessary to examine the functional relations between ERP components and EEG gamma activity.

Acknowledgements

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