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Short communication

Amplitude differences of evoked alpha and gamma oscillations in two different age groups

Diana Böttger, Christoph S. Herrmann*, D. Yves von Cramon

Max-Planck Institute of Cognitive Neuroscience, Postfach 500 355, 04303 Leipzig, Germany

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Abstract

The aim of this study was to investigate whether the amplitude of gamma-band activity is influenced by the factor age. We examined alpha- and gamma-band EEG activity and event-related potentials (ERPs) of 12 subjects. Six subjects constituted the younger (mean age = 36.6 years) and another six the older age group (mean age = 47.6 years). Subjects performed a visual discrimination task which required a response to Kanizsa squares (targets) among Kanizsa-triangles and non-Kanizsa figures. The ERPs of the younger group revealed a significantly larger N170 amplitude. The amplitudes of evoked alpha- and gamma-band activity were also found to be significantly higher in the younger group. We discuss the implications of these findings and possible reasons for a change of the oscillatory activity in the older age group.

Keywords: Aging; Binding; EEG; ERP; Gamma activity; Kanizsa figures; Illusory contours; Wavelet transform

1. Introduction

Oscillatory activity in the gamma frequency band (30–80 Hz) has been detected in various single-cell studies in animals (Gray et al., 1989; Eckhorn, 1994; Kreiter and Singer, 1996), as well as in several studies of the human electroencephalogram (EEG) (Basar-Eroglu et al., 1996a; Herrmann et al., 1999; Tallon-Baudry and Bertrand, 1999; Keil et al., 1999; Gruber et al., 2001) and magnetoencephalogram (Tallon-Baudry et al., 1997; Eulitz et al., 2000; Herrmann and Mecklinger, 2000; Kaiser et al., 2002). Functional mechanisms, which have been associated with this phenomenon include perceptual feature binding, memory and attentional processes (Gray et al., 1989; Basar-Eroglu et al., 1996b; Tallon-Baudry et al., 1998; Müller et al., 2000; Herrmann and Mecklinger, 2001). It is known that other features of the human EEG undergo significant changes during the lifetime of a subject. Examples include the P300 component of the ERP and activity in the alpha frequency band. The P300 shows a decreased amplitude, an increased latency and a shift of the scalp topography to a relatively more frontal distribution in elderly people (Polich and Luckritz, 1995; Tachibana et al., 1996; Friedman

*Corresponding author. Tel.: +49-341-9940-250; fax: +49-341-9940-113.
E-mail address: herrmann@cns.mpg.de (C.S. Herrmann).

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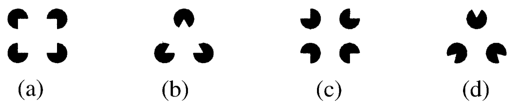

Fig. 1. The four stimuli: (a) Kanizsa square (target); (b) Kanizsa triangle; (c) non-Kanizsa square; and (d) non-Kanizsa triangle.

et al., 1997; Anderer et al., 1998). Age related changes of alpha-activity include a decrease of its frequency and amplitude (Obrist, 1976; Polich, 1997a,b). It is still unknown whether similar changes occur in the gamma-band of the human EEG. Therefore, we examined how gamma oscillations are influenced by the different age of subjects. Since we did not want to focus on maturation processes of children or aging affects in the elderly, we selected a group of middle-aged subjects.

2. Methods

2.1. Subjects

Twelve subjects with a mean age of 42.1 years (ranging from 31 to 49 years, seven female) participated in the study. All subjects were right-handed and had normal or corrected-to-normal vision. They showed no signs of neurological or psychiatric disorders and all gave written informed consent. The six youngest subjects constituted the younger group (mean age = 36.6 years) and the six oldest subjects (mean age = 47.6 years) the older group, respectively. Multiple experiments have revealed laterality differences of the gamma activity (Basar-Eroglu et al., 1996a; Haig et al., 1999; Lee et al., 2001). Therefore, we decided to present the stimuli in either one of the hemifields to further investigate laterality effects.

2.2. Stimuli and task

The stimuli used in this paradigm were composed of three or four inducer disks, which either constitute a Kanizsa figure, in our case a triangle or a square, due to their collinear arrangement or not (cf. Fig. 1). The Kanizsa square was the target in the experiment. The ratio of the radius of the inducer disks and the side-length of the illusory figures was 1/3. Stimuli subtended a visual angle of 1.5° including inducer disks (visual angle 0.7°) and were presented at an eccentricity of 3.14 degrees. Figures were displayed on a computer monitor (86.8 Hz) placed 1.5 m in front of the subjects.

Figures were displayed in black on white background for 1000 ms with a randomized stimulus onset asynchrony of 1500–3500 ms. The stimuli appeared in both halves of the visual field, on the left-hand and the right-hand side of a black fixation cross, which always remained in the middle of the screen. The experiment was run in four blocks with 200 stimuli per block. Each stimulus was presented in each half of the visual field 100 times. Left responders were instructed to push the left button with their left index finger if the target appeared and the right button with their right index finger if one of the three other figures was presented. Correspondingly, right responders had to use their right index finger for the target and their left one for all of the non-targets. Half of the subjects were right responders. The measurement of the reaction time was started with the onset of the figures.

2.3. Data acquisition

The EEG was recorded with NeuroScan amplifiers using 24 tin electrodes mounted in an elastic cap. Electrodes were placed according to the international 10–20 system. The ground electrode was C2 and all electrodes were referenced to the left mastoid (M1). Electrode impedance was kept below 5 kΩ. Horizontal and vertical EOG were registered with four additional electrodes. Data were sampled at 500 Hz and analogue-filtered with a 0.05-Hz high-pass and a 70-Hz low-pass filter. ERPs were low-pass filtered at 20 Hz for display.

2.4. Data analysis

In order to compute wavelet transforms of oscillatory activity, the original signal is convolved with a so-called wavelet. We computed the phase-locked (evoked) gamma response and the sum of activity (summed) separately. Non-phase-locked (induced) activity was calculated by subtracting phase-locked activity from the summed activity; for details see Herrmann et al. (1999).

Averaging epochs lasted from 300 ms before to 900 ms after stimulus onset. All epochs were visually inspected for artefacts and rejected if eye-movement artefacts or electrode drifts were visible. Baselines were computed in the −300–0-ms interval in each single trial and subtracted prior to computing the ERP averages. Trials in which a response error was made were rejected from the data, as well as trials in which the response time (RT) exceeded 2.5 standard deviations (S.D.) of the mean. RTs, error rates, ERP data, alpha and gamma activity were investigated for effects of the experimental conditions by means of a repeated measures analysis of variance across the two age groups (ANOVA). This ANOVA was conducted for five factors. The factor collinearity comprised the levels collinear and non-collinear. The factor shape consisted of the levels triangle and square. The factor hemisphere included the levels left and right hemisphere. The factor topography comprised the levels anterior and posterior. The factors hemisphere and topography formed four Regions of Interest. The factor field included the levels stimulus presented in the left or right half of the visual field. ERP components were defined as mean amplitudes in the following time intervals: 80–120 ms (P100), 130–180 ms (N170) and 350–500 ms (P300). The ERP amplitudes were defined on the basis of the grand mean of each group.

The gamma-components were defined as follows: 80–140 ms (early gamma) and 250–400 ms (late gamma). Definitions for the time windows of early and late gamma activity were derived from previous studies in our lab (Herrmann et al., 1999). The time interval of the alpha component was defined as: 100–200 ms.

3. Results

3.1. Behavioral data

The ANOVA of the RTs yielded a significant main effect of collinearity ($F_{1,10}=50.59$, $P<0.0001$) and for shape ($F_{1,10}=13.6$, $P<0.01$) indicating that the reaction time was longer for Kanizsa figures (522.83 ms) than for non-Kanizsa figures

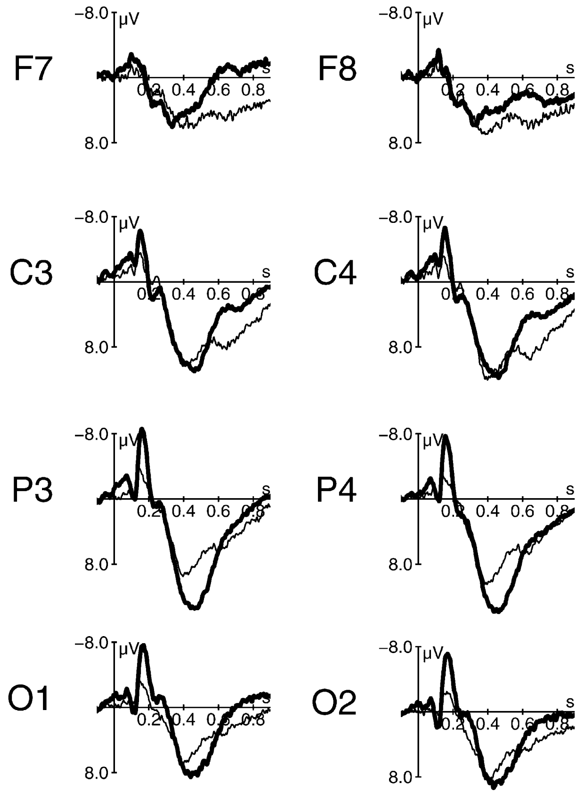

Fig. 2. ERPs (target condition) of the young group (thick) vs. the old group (thin) showing the higher amplitude in N170, as well as the prominent amplitude in P300 of the younger subjects.

(486.27 ms), and longer for squares (513.79 ms) than for triangles (495.31 ms). The ANOVA of the error rates yielded no significant effect, but they tended to show the same pattern as the RTs.

3.2. ERPs

The ANOVA over all 12 subjects in the P100 time interval yielded a significant main effect of field ($F_{1,10}=11.70$, $P<0.01$) and topography ($F_{1,10}=6.84$, $P<0.05$) but not of age.

In the N170 time interval the ANOVA showed a significant main effect of age ($F_{1,10}=9.25$, $P<0.05$), indicating a higher N170 amplitude in the younger group (−3.67 μV) compared to the older group (−1.28 μV) (cf. Fig. 2). Additionally, a significant main effect of topography ($F_{1,10}=6.49$,

$P<0.05$), a significant interaction of topography × collinearity ($F_{1,10}=17.33$, $P<0.01$) and a significant interaction of hemisphere × field ($F_{1,10}=21.19$, $P<0.01$) were found. Post-hoc comparisons yielded a significant effect of collinearity in the posterior region ($F_{1,10}=12.90$, $P<0.005$), indicating a higher N170 amplitude for Kanizsa figures (−4.26 μV) than for non-Kanizsa figures (−3.57 μV). Post-hoc comparisons also yielded a significant effect of field in both the left ($F_{1,10}=22.70$, $P<0.001$) and right hemisphere ($F_{1,10}=13.87$, $P<0.005$), indicating a higher N170 amplitude in the left hemisphere after stimulation in the right visual field (−3.53 μV) as compared to stimulation in the left visual field (−1.93 μV) and a higher N170 amplitude in the right hemisphere after stimulation in the left hemifield (−3.35 μV) vs. stimulation in the right hemifield (−1.07 μV).

The ERPs showed a typical P300 which was higher for the target than for the non-targets. We could find a significant main effect of collinearity ($F_{1,10}=19.05$, $P<0.001$) and shape ($F_{1,10}=8.97$, $P<0.05$) in this time interval, indicating that P300 amplitudes were larger for Kanizsa figures (6.08 μV) than for non-Kanizsa figures (5.21 μV) and larger for squares (6.11 μV) than for triangles (5.18 μV). No effect of age was found for the P300 amplitude.

3.3. Alpha

The ANOVA of the alpha activity yielded a significant main effect of age ($F_{1,10}=5.77$, $P<0.05$), reflecting the higher activity of younger subjects (0.86 μV) as compared to the older ones (0.46 μV) (cf. Fig. 3). We also found significant main effects of topography ($F_{1,10}=11.96$, $P<0.01$) and collinearity ($F_{1,10}=8.17$, $P<0.05$), indicating that the activity was higher in posterior regions (0.95 μV) than in anterior regions (0.38 μV) and higher for Kanizsa figures (0.74 μV) than for non-Kanizsa figures (0.59 μV).

3.4. Gamma

We found a significant main effect of age ($F_{1,10}=6.48$, $P<0.05$) in the early time window

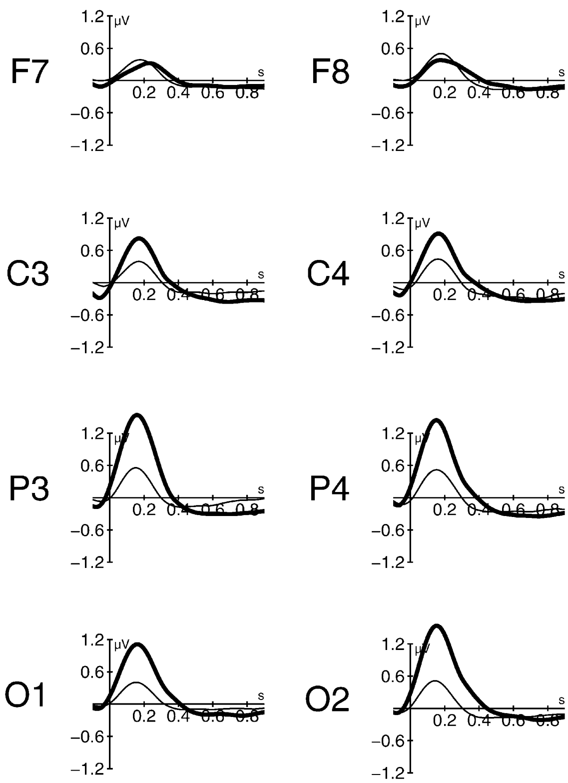

Fig. 3. Evoked alpha activity of the young group (thick) compared to the old group (thin). Both age groups revealed smaller alpha amplitudes in anterior electrodes as compared to posterior ones.

of the evoked gamma activity, indicating a higher amplitude of evoked gamma activity for the younger subjects (0.18 μV) as compared to the older ones (0.06 μV) (cf. Figs. 4 and 5). There was no significant difference of summed activity between younger and older subjects ($F_{1,10}=2.66$, $P<0.1$). The ANOVA also yielded a significant interaction of hemisphere × topography × field ($F_{1,10}=32.15$, $P<0.0005$). Post-hoc comparisons showed a significant effect of field in the right anterior Region of Interest ($F_{1,10}=6.45$, $P<0.05$). There was no significant effect in the late time interval and no significant influence of any other factor.

4. Discussion

The behavioral data show a typical pattern of target discrimination in RTs as well as in error

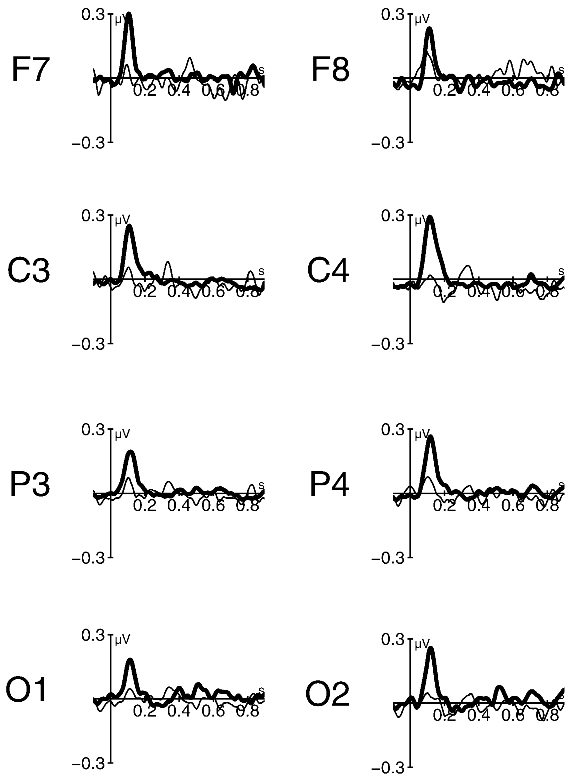

Fig. 4. Evoked gamma activity of the young group (thick) compared to the old group (thin). No decrease of amplitude in anterior electrodes was present.

rates. As expected, the target, which occurs less frequently than the non-targets, is processed slowest (Teichner and Krebs, 1974). As in a previous experiment by Herrmann and Mecklinger (2000), this was also the case when the Kanizsa square was the target, which would otherwise be expected to be processed faster than a non-Kanizsa square due to its figural features (Pomerantz, 1983). We did not detect a difference of RTs or error rates between younger and older subjects, probably due to the relatively small difference in age.

Nevertheless, there was an effect of age seen in the ERPs. We found a decreased N170 amplitude in the older group, which is consistent with previous studies about ERPs in older subjects (Polich and Luckritz, 1995; Tachibana et al., 1996; Friedman et al., 1997; Anderer et al., 1998). As expected, there was a significant main effect of field visible in the P100 as well as in the N170 time interval, due to visual stimulation in hemifields. Stimuli in the right half of the visual field are processed in the left hemisphere first and the stimuli in the left half of the visual field in the right hemisphere, respectively. The P300-topography is more central, using information from both sides of the primary cortex, and therefore, showed no field effect. We found no significant differences in the P300 time window between the two age groups. However, we noticed a tendency of a higher P300 amplitude in the younger group, which is visible at electrodes P3 and P4 in Fig. 2. This is consistent with the literature showing a decreased amplitude and prolonged latency of the P300 component in the elderly (Polich, 1997b).

The amplitude of the evoked alpha activity was significantly lower in the older age group consistent with previous studies discussing changes of alpha oscillations in aging (Polich, 1997a,b). Interestingly, we found a significant main effect of collinearity in this frequency band. According to Sewards and Sewards (1999), static objects are, at least in part, represented by synchronized alpha-band oscillations. The authors suggest that both alpha and gamma-band oscillations are correlated and necessary to constitute visual awareness, but are generated independently. Our findings support

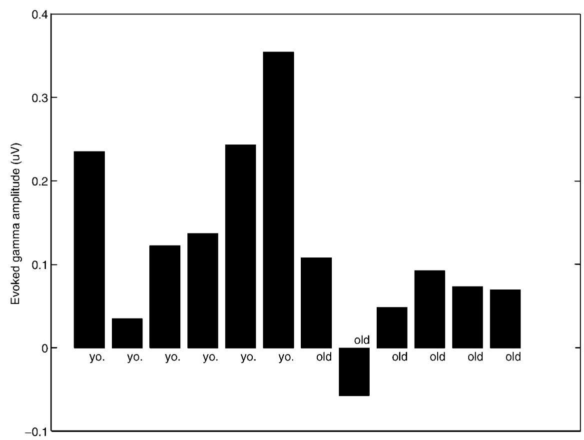

Fig. 5. Amplitude of the early evoked gamma activity (μV) of individual subjects of the younger (yo) and older (old) groups.

this hypothesis. The activity of alpha oscillations was highest in posterior regions. In contrast, the topographical analysis of the gamma-activity revealed activation at occipital and frontal sites. We found no significant main effect of collinearity and shape in the gamma band, whereas a significant main effect of collinearity was found in the alpha frequency range. Another difference between alpha and gamma activity became obvious in the wavelet transforms of our data. We identified a peak in the gamma-frequency range between 40 and 50 Hz in the younger group, which was not detectable in the older group. Taking into account the different topographical distribution, the different functional correlations and the additional 40 Hz component in the time–frequency diagram of the younger subjects, we assume that the gamma oscillations found in this study are not merely a secondary product of alpha activity.

An interesting question raised by these findings is why less gamma-activity was detected in the older group, while the behavioral parameters showed no difference compared to the younger subjects. The early gamma response represents evoked activity, which means it is phase-locked to stimulus onset. If there is a loss of ability to synchronize to a stimulus in the older group, the phase-locked, but not the summed activity, would be smaller. Indeed the ANOVA of the overall activity of old and young subjects yielded no significant difference. Therefore, a decrease of phase-locking rather than a decreased amplitude of gamma activity might have caused the age effect in this study.

Another question we want to discuss is, which cognitive processes might be reflected by the two distinct responses in the alpha and gamma-band. The alpha-activity showed a correlation with the collinearity of the stimulus. Therefore, we assume it represents a cognitive process, which is important for distinguishing Kanizsa from non-Kanizsa figures. Activity in the alpha-frequency range has been associated with a variety of cognitive functions, such as memory performance, anticipation, attentional, sensory and motor processes (Klimesch et al., 1993; Klimesch, 1997; Basar et al., 1997). In contrast, the statistical analysis of early-evoked gamma-activity showed no correlation with stimulus features, but with the field of presentation. Hence, its functional role seems to be connected with early modulation of sensory information, which is consistent with a study by Karakas and Basar (1998). The lack of correlation with the Gestalt features of the Kanizsa stimuli is in contrast to an experiment of Herrmann and Mecklinger (2001). A possible reason might have been the lateralized presentation of smaller stimuli in this study, which could have reduced their salience. Gamma band activity has been shown to depend upon the size of stimuli (Edwards et al., 2001).

The amplitude of the early evoked gamma activity in the younger group was found to be significantly higher than in the older group. This finding was surprising, considering the fact that there was no difference in the behavioral parameters. The sum of induced and evoked gamma activity (summed activity), on the other hand, showed no age effect. However, there was no clear peak of summed gamma activity in this paradigm. Therefore, the effect of the two age groups onto summed gamma activity remains unclear. Further studies with subjects of a wider age range are necessary to investigate the connection between aging and changing of oscillatory activity in the brain and to explain the functional significance of this process.

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