

Stimulus dependence of human gamma band activity

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Introduction

The human event-related potential (ERP) shows short bursts of 40 Hz (gamma) activity around 100 ms after stimulus onset (Tallon, 1995). Some experiments reported that these early gamma responses reflect cognitive processes (Herrmann et al., 1999; Herrmann & Mecklinger, 2001). Others were

not able to find differences in evoked gamma activity between different cognitive conditions (Karakas et al., 1998). The objective of this experiment was to find out which physical stimulus parameters modulate the amplitude of evoked gamma activity in addition to the reported cognitive factors.

Methods

Subjects

We recorded EEG from 7 subjects while they performed a visual discrimination task. 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 to participate in the study.

Stimuli

The stimuli used in this paradigm were composed of three or four inducer disks which constitute a Kanizsa figure due to their collinear arrangement. The stimuli varied across the two dimensions shape and size. I.e. they were either triangular or square in shape and either small or large in size (cf. Figure 1). Small and large stimuli subtended a visual angle of 1.8 and 5.4 degrees, respectively. The ratio of the radius of the inducer disks and the side-length of the illusory figures was 1/4. They were presented on a computer monitor 1m in front of the subjects.

Data acquisition

The EEG was recorded with NeuroScan amplifiers using 64 tin electrodes mounted in an elastic cap. Electrodes were placed according to the international 10-10 system. The ground electrode was placed near the left mastoid (M1) and all electrodes were referenced to the left mastoid. Electrode impedance was kept below 5kΩ. Horizontal and vertical electrooculogram (EOG) recordings were registered with four additional electrodes. Data were sampled at 256 Hz and analog-filtered with a 0.05 Hz high-pass and a 100 Hz low-pass filter. An additional, digital 25 Hz low-pass filter was applied before displaying the ERP data.

Data analysis

Averaging epochs lasted from 200 ms before to 800 ms after stimulus onset. All epochs were visually inspected for artefacts and rejected if eye movement artefacts, muscle artefacts or electrode drifts were visible. Baselines were computed in the -200 ms to 0 ms interval in each single trial and subtracted prior to computing the event-related potential (ERP) averages.

For the analysis of gamma activity, a wavelet transform based on Morlet wavelets was employed (Herrmann et al., 1999).

Statistics

In order to avoid a loss of statistical power that is inherent when repeated measures ANOVAs are used to quantify multi-channel EEG data, posterior electrode sites were pooled to a topographical regions of interest (ROIs). For statistical analyses, ERP amplitudes were pooled across parietal, occipital and parieto-occipital electrodes into one ROI. ERP components were defined as mean amplitudes in the following time intervals: 80-120 ms (P1) and 120-170 ms (N1). Gamma activity was defined as the mean amplitude in the time interval 50-100 ms pooled across electrodes (FC3, FC4, FCZ, C3, C4, CZ, P3, P4, P7, P8, PZ, PO3, PO4, PO7, PO8, POZ).

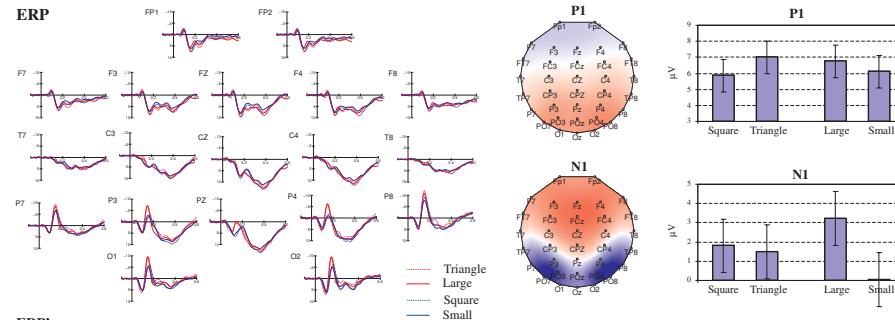
EEG data was analyzed with a repeated measures ANOVA: The two stimulus dimensions shape and size were used as factors with levels square vs. triangle and small vs. large, respectively.

The stimuli were presented for 700 ms with randomized inter-trial-intervals ranging from 1000 to 1500 ms. Figures were displayed in black together with a black central fixation cross on white background.

Subjects were instructed to respond to Kanizsa squares of any size with a response of their right index finger on one button and to Kanizsa triangles of any size with their left index finger on another button. The four stimulus types were presented equally probable in a pseudo-randomized order resulting in a target probability of 0.5.

Results

2A

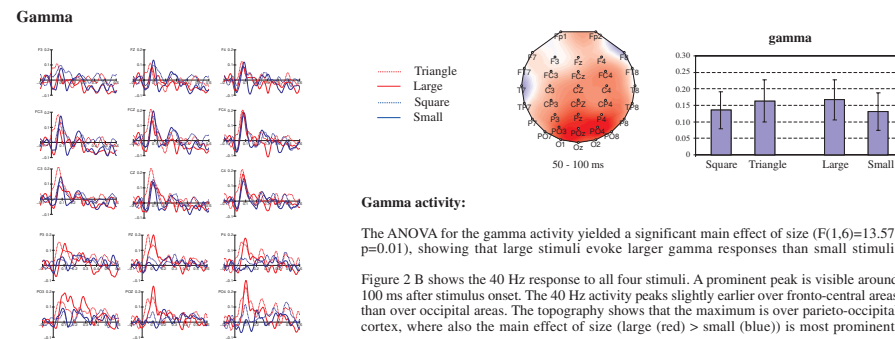


ERP's:

The ANOVA revealed a significant main effect of form ($F(1,6)=7.55, p<0.05$) for the P1 time interval, indicating larger amplitudes for triangles than for squares. For the N1 time interval, the ANOVA revealed a significant main effect of size ($F(1,6)=25.05, p<0.005$). Large stimuli evoked larger N1 components than small ones.

Figure 2 shows the ERPs in response to all four stimuli. Clear P1, N1 and P3 peaks are visible. P1 is larger for triangles (dotted) than squares (solid) while N1 is larger for large (red) than small (blue) stimuli. A P3 was generated for all stimuli, since every stimulus required a response. Topographies of N1 and P1 reveal that these components are strongest over posterior cortex.

2B



Gamma activity:

The ANOVA for the gamma activity yielded a significant main effect of size ($F(1,6)=13.57, p=0.01$), showing that large stimuli evoke larger gamma responses than small stimuli.

Figure 2 B shows the 40 Hz response to all four stimuli. A prominent peak is visible around 100 ms after stimulus onset. The 40 Hz activity peaks slightly earlier over fronto-central areas than over occipital areas. The topography shows that the maximum is over parieto-occipital cortex, where also the main effect of size (large (red) > small (blue)) is most prominent.

Discussion

We demonstrated the dependency of P1, N1 and gamma activity upon physical stimulus parameters. While P1 (80-120 ms) and gamma activity (50-100 ms) appear at a similar latency, they are influenced by different stimulus properties. The P1 is mainly influenced by the shape of a stimulus whereas the gamma activity is modulated by its size. The factor size subsequently also influences the amplitude of the N1.

For the early ERP components it has long been known that they are mainly affected by physical stimulus parameters which is why they were considered exogenous components (Coles & Rugg, 1995). But recent papers show that perceptual parameters (endogenous factors) can also modulate the N1 component (Kaernbach et al., 1999; Herrmann & Bosch, 2001).

The effects of exogenous variations on early ERP components are usually larger in amplitude than are the cognitive ones. This leads us to assume that the exogenous factors probably regulate the overall amplitude of early components while endogenous factors result in more subtle changes of the amplitude. These small changes can only be observed if the overall amplitude is sufficiently large to guarantee a good signal-to-noise ratio. Therefore, we suggest to use large intense stimuli which evoke amplitudes large enough to observe endogenous variation in addition to the exogenous ones.

The above seems to be true not only for ERP components but also for early evoked gamma responses (and maybe other oscillatory activity). While Herrmann et al. (1999) found cognitive effects on the early evoked gamma response with black stimuli on white background (high contrast), Tallon et al. (1995) did not observe this effect with very similar stimuli which were presented in gray (lower contrast). Therefore, it seems plausible to assume that exogenous factors may be the cause of different results in gamma experiments. We suggest to use stimuli which are large (up to 5 degrees of visual angle to fit into the macular region of the retina), high in contrast and sufficiently long in duration to avoid an overlap of onset and offset responses.

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