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# Cortical responsiveness is reduced during P300 potential. Does the level of initial activity affect this inhibition?

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**Abstract.** The regulation of firing thresholds of cortical pyramidal cells has been suggested as one of the mechanisms underlying the generation of the P300 component of the human event-related potential. According to this hypothesis, the detection of an important stimulus produces a widespread inhibition of "irrelevant" networks, interrupting the ongoing cortical activity and facilitating the analysis of the important information. In the present experiment, target stimuli in a standard "odd-ball" paradigm were used as important events. The cortical responsiveness was measured using the responses to additional probing stimuli delivered 400 ms and 1,000 ms after target and non-target stimuli. The subjects were asked to count mentally the target stimuli and ignore the non-targets and the probes. The level of "irrelevant" cortical activity was manipulated using additional visual noise stimulation. Event-related potentials were recorded at Fz, Cz, Pz and Oz scalp sites. Our results showed that the noise reduced the initial responses to target and non-target stimuli in Oz, Pz and Cz but not in Fz recordings. The noise reduced the probe responses in Oz and Pz but not in Cz and Fz recordings. The amplitudes of P300 components were not affected by the noise. The target stimuli reduced the subsequent probe responses in Pz and Cz but not in Oz and Fz recordings. Thus, the effects of noise and target detection were not identical in the different regions of cortex. The other important outcome of our study was that the target stimuli suppressed the effects of noise. The effect of noise on probe responses was significant in the non-target but not in the target trials. The effect of noise was significant if the probes were delivered 1,000 ms after "odd-ball" stimuli, but it was insignificant when the delay was only 400 ms. Such results support the hypothesis that important information reduces cortical responses to other, irrelevant stimuli.

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**Key words:** visual event-related potentials, inhibitory effect of P300, "relevant" and "irrelevant" activity in the cortex

## INTRODUCTION

The large number of mutual excitatory connections between cortical neurons can easily produce uncontrolled activation. To avoid this, the excitability of cortical cells should be controlled. A mechanism for such control was suggested by Elbert and Rockstroh (1987) (Elbert 1993). According to their hypothesis, information about the amount of ongoing cortical activity is projected *via* the basal ganglia to the thalamus. From the thalamus, the information is sent back to the apical dendrites of cortical pyramidal cells. The regulation of cortical excitability is achieved by controlling the polarization of these dendrites. Since the thalamocortical afferent system is controlled by the mediotthalamic-frontocortical system which is probably involved in the attentive behavior (Skinner and Yingling 1977) Elbert and Rockstroh suggested that the "importance" or "relevance" of incoming stimulus could affect the level of cortical excitability. They suggested that the important stimuli produced the hyperpolarizing input to apical dendrites of cortical pyramidal cells thus elevating their firing thresholds. The authors speculated that such inhibitory signal could interrupt the ongoing cortical activity and improve the contrast between the assemblies of responding neurons and the silenced background.

The P300 component of the human event-related potential can provide an indicator of "important" stimuli. This large, positive wave can be recorded only in response to stimuli that are either relevant for the task, or at least rare and different from the other frequent stimuli. (Donchin and Coles 1988, Verleger 1988). Animal experiments with simultaneous recordings from single neurons and from the surface of the skull indicated that the main source of high amplitude, positive waves was the hyperpolarization of apical dendrites of cortical pyramidal cells (Birbaumer et al. 1990, Caspers et al. 1980, Creutzfeldt 1983, Rockstroh et al. 1989, Speckmann et al. 1984). Thus, Elbert and Rockstroh suggested that the P300 potential could reflect the inhibition of irrelevant neurons after the advent of an important stimulus. It should be noted that the Elbert and Rockstroh hypothesis did not contradict earlier theories explaining the generation of P300 potential at the psychological level (Donchin and Coles 1988, Verleger 1988). It rather suggested one of the physiological mechanisms underlying complex psychological phenomena.

The responsiveness of the cortex could be tested by measuring the responses to additional "probing" stimuli

delivered with different delays after the detection of an important stimulus. The first observation of an inhibitory phase during P300 potential was achieved in the auditory system: Rockstroh and coauthors (1992) showed that the responses to secondary probe stimuli were inhibited during the P300 potential. For the continuous monitoring of cortical responsiveness the same authors used the auditory steady-state responses (Fourier components of the EEG signal that followed the frequency of continuous, periodic stimulation). The steady-state responses were reduced after detection of an important stimulus (Rockstroh et al. 1996). More recent studies on the visual system supported the results of the auditory experiments (Michalski 2001). In addition, the experiments on the visual system indicated that inhibitory effects of important stimulus detection were much stronger in the occipital and parietal recordings than in the frontal recordings.

In the present experiment, an attempt was made to manipulate the level of "irrelevant" cortical activity. The "irrelevant" activity, according to Elbert and Rockstroh theory, should be inhibited when the "relevant" stimulus is detected. A large field stimulation with visual noise was used to increase the "irrelevant" activation. The effects of noise stimulation on neuronal activity in the lower order cortical fields are relatively well known in cats and monkeys. They consist of a slight but significant increase of neuronal activity (Skottun et al. 1988, Squatrito et al. 1990) and a reduction of responses to other, discrete stimuli such as slits of light (Allman et al. 1990, Blakemore and Tobin 1972, Born and Tootell 1991, DeAngelis et al. 1994, Gulyas et al. 1987, Hammond and MacKay 1975, Knierim and Van Essen 1992, Li and Li 1994, Orban et al. 1979, Sengpiel et al. 1997, Squatrito et al. 1990). In the present experiment the effect of noise on human event-related potentials was measured and the alterations of this effect after presentation of "relevant" stimuli were analyzed. The "relevant" stimuli were indexed by P300 waves. The inhibition of "irrelevant" cortical activity after advent of important stimuli should result in the reduction or cancellation of the effect of noise.

## METHODS

Data were collected from 15 volunteers of both sexes (11 females and 4 males), aged 25-48 years (mean = 35, SD = 7.8). Informed consent was obtained from all participants.

EEG signals were recorded with disc electrodes glued at Fz, Cz, Pz and Oz (in the middle between O1 and O2) positions, referenced to linked mastoids and supplemented by vertical and horizontal EOG. The signals were sampled with 2,048 Hz frequency, 12 bit resolution, digitally filtered 0.16-30 Hz and reduced to 256 Hz by averaging the adjacent points (Elmiko Paperless EEG system). The data were stored in epochs containing 250 ms before and 1.5 s after the stimulus onset. The epochs were rejected by a computer program if EOG amplitude exceeded 40  $\mu$ V. The rejected epochs were replaced with the new ones.

The yellow, red and green rectangles were used as stimuli (2 deg  $\times$  2 deg of the visual angle, 10 cd/m<sup>2</sup> luminosity, 100 ms duration). A mosaic of color LED diodes inserted side by side into a transparent plate was used to produce these stimuli in the same spatial location, in a center of 21 inch TV screen.

The yellow and red rectangles were used as stimuli in a standard "odd-ball" procedure. The subjects were asked to count mentally the yellow rectangles (targets) and report their number at the end of recording. The data were rejected if the error in counting was bigger than 20%. The subjects were asked to ignore the red rectangles (non-targets). The "odd-ball" stimuli were presented every 2.5 s. The probability of appearance of the target stimulus was 0.12.

Flashes of the green rectangle were used as probes. They followed both the target and the non-target "odd-ball" stimuli. The subjects were instructed to ignore these stimuli. Separate blocks of recordings were obtained with the probes delivered 400 ms, and 1,000 ms after "odd-ball" stimuli.

All recordings were repeated twice: with the TV screen displaying a visual noise of 0.2 cd/m<sup>2</sup> averaged luminosity and with an uniform background of the same luminosity. The noise pattern was obtained by setting the TV receiver (Panasonic TC-21S1RPC) to full contrast without an input signal. For the recordings without the noise, the TV screen was darkened and covered with a gray paper to adjust luminosity.

The epochs of EEG were averaged, stored and printed using Elmiko software package. To ensure the proper measurement of probe responses, the minimum of 60 good target stimulus repetitions were averaged. The amplitudes and the latencies of peaks were measured using a cursor on the computer screen and data were transferred to SYSTAT program for multi-factor analysis of variance (ANOVA). In addition, the grand-averaged

waveforms were computed by averaging data for all subjects in each experimental condition.

## RESULTS

Figure 1 shows the grand-averaged potentials evoked by target and non-target stimuli followed by probes presented 400 ms and 1,000 ms later. Three components can be clearly distinguished in the averaged potentials: (i) early responses to target or non-target stimuli with the dominating P200 waves; (ii) P300 waves in responses to target stimuli; (iii) responses to probes. The peak amplitudes and the latencies of these components were measured and used for statistical analysis.

Figure 1 indicates that responses to probes delivered shortly after target stimuli were suppressed in Cz, Pz and Oz recordings (compare responses to probes presented after target and non-target stimuli or compare responses to probes presented 400 ms and 1,000 ms after target stimuli). Probe responses were less attenuated in Fz recordings. Instead, the comparison of responses to probes presented 400 ms after target and non-target stimuli indicates that the latencies of these responses were elongated as the result of their interaction with P300 waves (thin arrow shows the relevant region of Fig. 1). All these effects can be seen in the recordings obtained both with the uniform background and with the visual noise.

### Early responses

The amplitudes of the P200 components were measured from the averaged voltage level during the 250 ms pre-stimulus period. The mean values of these amplitudes, recorded in the different experimental conditions, are shown in Fig. 2. Three-way ANOVA (electrode  $\times$  target  $\times$  noise) was used for statistical evaluation of the results. Figure 2 shows that the noise clearly reduced the amplitudes of early components, both in responses to the target and the non-target stimuli. The effect was highly significant ( $F_{1,448}=27.258$ ,  $P<0.001$ ). Figure 2 also indicates that the early components were bigger in responses to the target stimuli than in responses to the non-targets. This difference was also highly significant ( $F_{1,448}=50.241$ ,  $P<0.001$ ). Finally, the amplitudes of early components differed between the electrodes ( $F_{3,448}=29.557$ ,  $P<0.001$ ).

The amplitudes of early components recorded with each electrode were analyzed separately with two-way

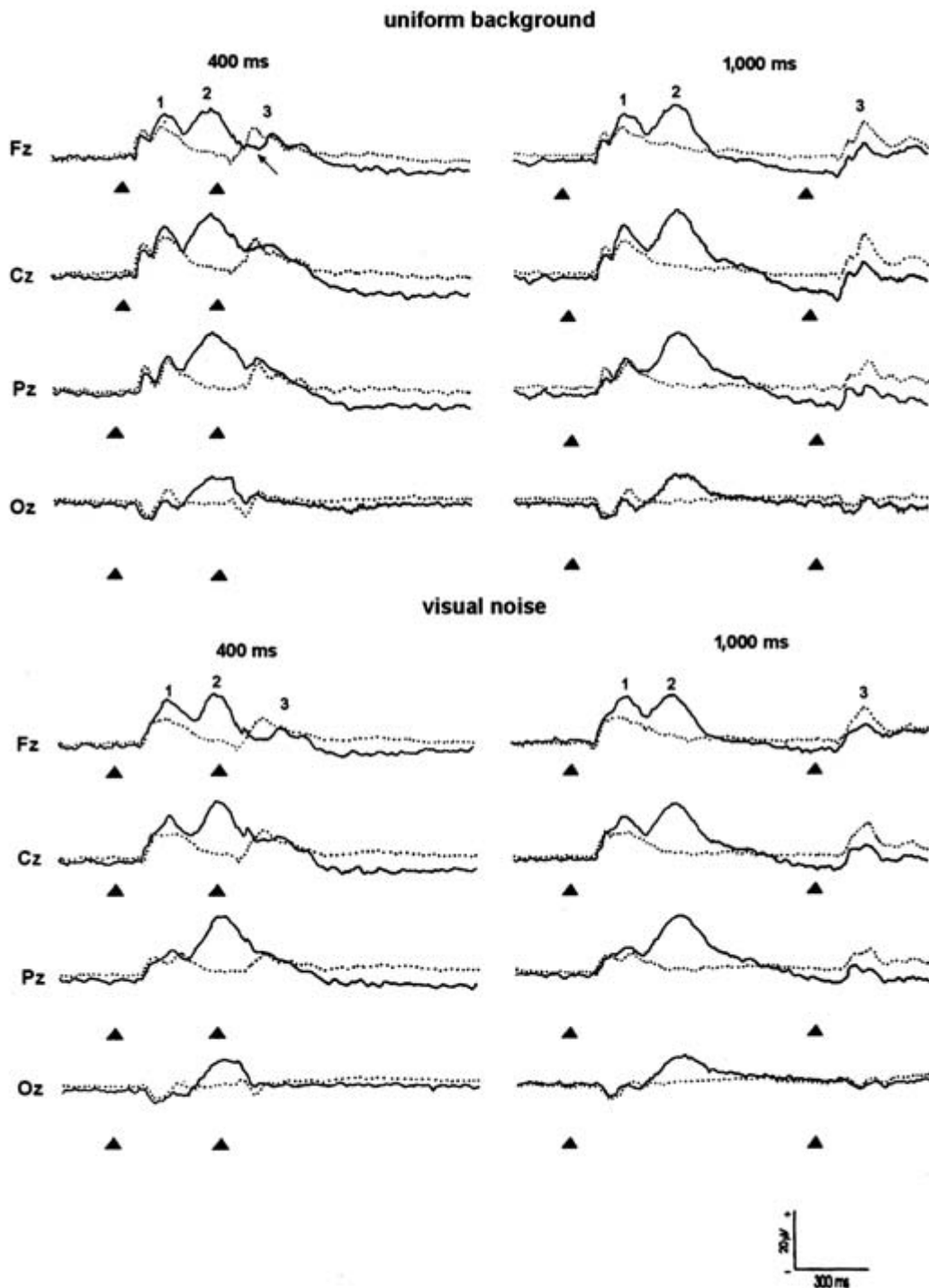


Fig 1. Grand-averaged responses to visual "odd-ball" and probe stimuli. Upper block shows the potentials recorded with the "odd-ball" and probe stimuli displayed on a uniform background. Lower block shows the potentials recorded with the same stimuli displayed on a background of visual noise. The probes were presented 400 ms (left column) and 1,000 ms (right column) after the onset of "odd-ball" stimuli. Rows of the figure show the different electrode recordings. Solid lines show the responses to target stimuli and dotted lines show the responses to non-target stimuli. The first black triangle indicates the onset of the "odd-ball" stimulus. The second black triangle indicates the onset of the probe. The main ERP components are labeled above Fz recordings: (1) early responses to "odd-ball" stimuli; (2) P300 waves; (3) responses to probes. The thin arrow shows the effect of target stimuli on probe response latency in Fz recordings.

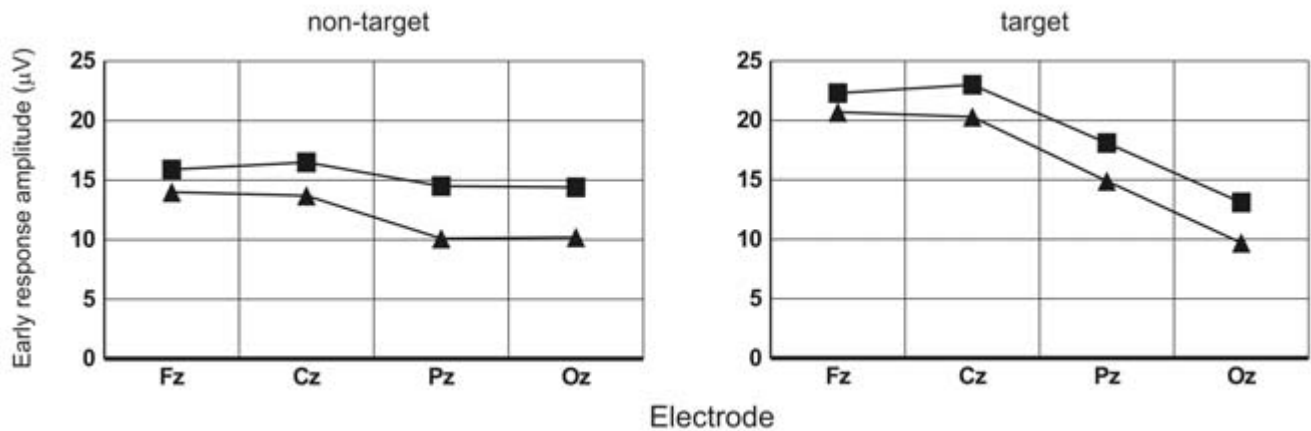


Fig. 2. Mean amplitudes of P200 components in the early responses to "odd-ball" stimuli recorded with the different electrodes. The left graph shows the amplitudes of responses to non-target stimuli and the right graph shows the responses to target stimuli. The squares show the mean amplitudes recorded with the uniform background and the triangles show the amplitudes recorded with the visual noise.

ANOVA (target  $\times$  noise). The effect of noise was highly significant in Oz and Pz recordings, just significant in Cz and insignificant in Fz recordings ( $F_{1,112}=12.669$ ,  $P<0.001$  in Oz;  $F_{1,112}=16.148$ ,  $P<0.001$  in Pz;  $F_{1,112}=4.966$ ,  $P<0.028$  in Cz). In contrast, the effect of target detection was significant in Fz, Cz and Pz but insignificant in Oz recordings ( $F_{1,112}=19.385$ ,  $P<0.001$  in Pz;  $F_{1,112}=28.262$ ,  $P<0.001$  in Cz;  $F_{1,112}=23.649$ ,  $P<0.001$  in Fz).

The latencies of early responses were also analyzed with three-way ANOVA (electrode  $\times$  target  $\times$  noise). No significant effects were found.

### P300 components

Clear P300 waves were recorded in all subjects. Their peak amplitudes were measured from the averaged pre-stimulus level. The amplitudes were analyzed with three-way ANOVA (electrode  $\times$  delay  $\times$  noise). The delay variable was introduced because it could not be excluded that the interactions with short delay probes would affect the P300 falling slopes and the peak amplitudes. The statistical analysis showed that the only significant effect was the difference between the electrodes ( $F_{3,224}=25.060$ ,  $P<0.001$ ).

The latencies of P300 peaks were analyzed with a similar three-way ANOVA (electrode  $\times$  delay  $\times$  noise). The effect of noise on P300 peak latency was insignificant. The latencies of P300 peaks were significantly shorter when these waves were followed by the responses to short delay probes ( $F_{1,218}=7.760$ ,  $P<0.006$ ).

Apparently the incoming probe stimuli affected the falling slopes of P300 waves in such a way that their peak amplitudes were detected earlier.

The falling slopes of P300 waves were analyzed by measuring the time in which the voltage was reduced to 50% of the peak value (falling time). Three-way ANOVA (delay  $\times$  electrode  $\times$  noise) was used for the statistical evaluation. The falling time was elongated by the noise ( $F_{1,192}=5.051$ ,  $P<0.026$ ). On the other hand, the falling time was shorter when P300 wave was followed by the response to short delay probe ( $F_{1,192}=7.297$ ,  $P<0.008$ ). Finally, the falling time differed between the electrodes ( $F_{3,192}=4.068$ ,  $P<0.008$ ).

### Responses to probes

The responses to probes could arise from very different voltage levels (such as the slopes of P300 waves). Thus, the amplitudes of these responses were measured from the level immediately preceding their rising slopes. The amplitudes were analyzed with four-way ANOVA (electrode  $\times$  target  $\times$  delay  $\times$  noise). All four variables produced significant effects ( $F_{3,447}=19.986$ ,  $P<0.001$  for the electrodes;  $F_{1,447}=52.180$ ,  $P<0.001$  for the delay;  $F_{1,447}=24.732$ ,  $P<0.001$  for the target;  $F_{1,447}=9.375$ ,  $P<0.002$  for the noise). There was also a significant interaction between the target and the delay variables ( $F_{1,447}=24.732$ ,  $P<0.001$ ). Figure 3 shows the mean amplitudes of responses to probes presented 400 ms and 1,000 ms after the target and the non-target stimuli. Two curves in each graph show the data obtained



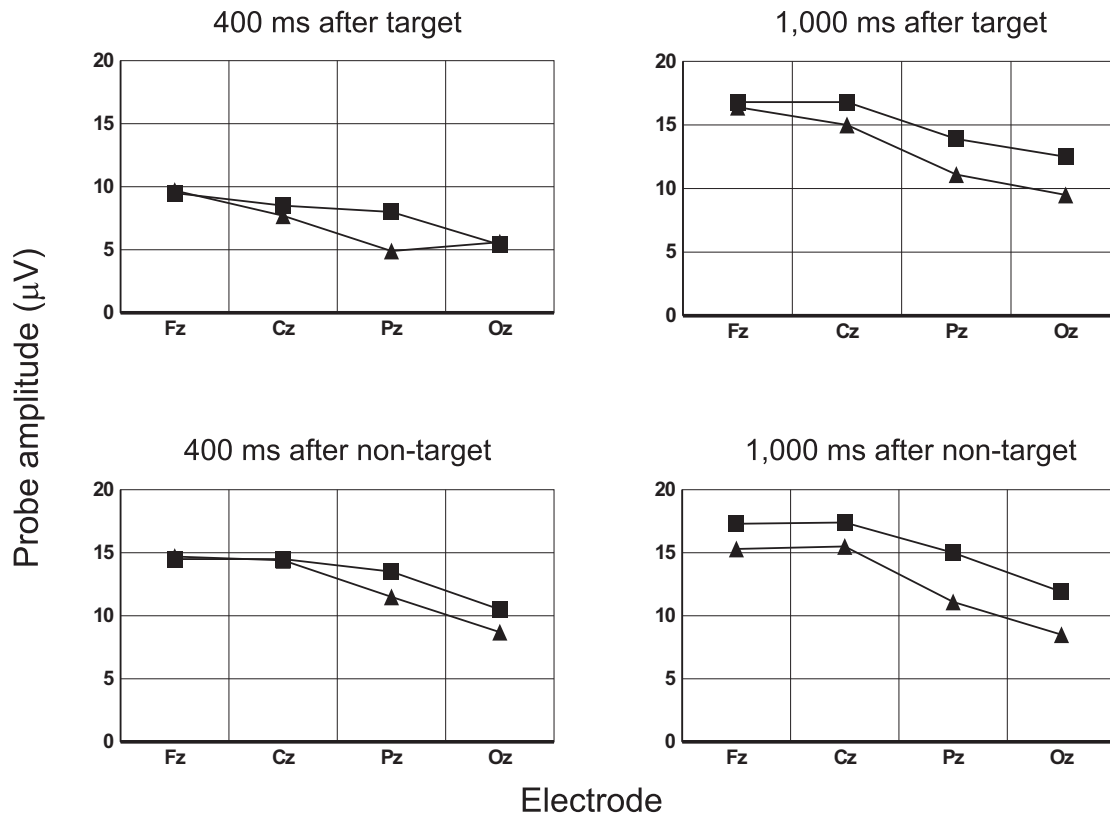


Fig. 3. Mean amplitudes of P200 components in the probe responses that followed the target (upper row) and the non-target (lower row) stimuli. In separate blocks of recordings, the probes were presented 400 ms (left column) and 1,000 ms (right column) after the "odd-ball" stimuli. The squares show the amplitudes recorded with the uniform background and the triangles show the amplitudes recorded with the visual noise.

with and without the background noise stimulation. Figure 3 indicates that: (i) responses to probes presented 400 ms after target stimuli were reduced; (ii) responses to probes recorded with background noise stimulation were reduced; (iii) effects of noise were stronger in Oz and Pz and weaker in Cz and Fz recordings.

The amplitudes of probe responses recorded with each electrode were analyzed separately with a three-way ANOVA (target  $\times$  delay  $\times$  noise). In Fz recordings, the effect of noise was insignificant. The effect of target was close to the level of statistical significance but did not reach it ( $P < 0.06$ ). In Cz recordings, both the effect of target and the effect of delay were significant ( $F_{1,112} = 9.635$ ,  $P < 0.002$  for target;  $F_{1,112} = 19.951$ ,  $P < 0.001$  for delay). In addition, the interaction between the target and the delay was significant ( $F_{1,112} = 6.862$ ,  $P < 0.01$ ). Since it was assumed that a short delay was necessary to enable an interaction of probe responses with P300 wave, this pattern of significant effects pro-

vided a strong clue that target detection affected the amplitudes of probe responses. In contrast, the effect of noise was insignificant in Cz recordings. In Pz recordings, the same pattern of significant effects – target, delay and their interaction – indicated the suppressive effect of target detection on the probe responses ( $F_{1,112} = 12.417$ ,  $P < 0.001$  for target;  $F_{1,112} = 12.654$ ,  $P < 0.001$  for delay;  $F_{1,112} = 8.519$ ,  $P < 0.004$  for their interaction). But, in contrast to Fz and Cz data, the suppressive effect of noise was also significant in Pz recordings ( $F_{1,112} = 10.035$ ,  $P < 0.002$ ). In Oz recordings, only the effect of noise was significant ( $F_{1,112} = 4.005$ ,  $P < 0.048$ ). The target variable failed to produce any significant effect. However, the effect of target detection was significant in Oz recordings in the absence of noise ( $F_{1,28} = 5.118$ ,  $P < 0.032$ ).

To reveal the possible changes in the effects of noise after the advent of an important stimulus the amplitudes of probe responses recorded after target and non-target

stimuli were analyzed separately using a three-way ANOVA (delay  $\times$  electrode  $\times$  noise). Only the responses to probes presented after non-target stimuli were significantly reduced by the noise ( $F_{1,224}=5.62$ ,  $P<0.019$ ). The effect of noise on responses to probes presented after target stimuli was insignificant. As an alternative approach, the responses to probes presented 400 ms and 1,000 ms after "odd-ball" stimuli were analyzed separately with a three-way ANOVA (electrode  $\times$  noise  $\times$  target). At the short delay, the effect of target was highly significant ( $F_{1,223}=49.930$ ,  $P<0.001$ ) and the effect of noise was insignificant. At the long delay, the effect of target was insignificant and the effect of noise became highly significant ( $F_{1,224}=9.899$ ,  $P<0.002$ ).

The latencies of probe responses were analyzed with four-way ANOVA (delay  $\times$  electrode  $\times$  target  $\times$  noise). The latencies were significantly elongated after target stimuli ( $F_{1,426}=5.07$ ,  $P<0.025$ ) but the effect of noise was insignificant.

## DISCUSSION

The present experiment was designed to study the effect of the advent of important information on cortical responsiveness. The electrode montage was typical for P300 studies. With the exception of Oz, these electrodes ensured the recording of high amplitude P300 waves and facilitated the detailed analysis of their interactions with probe responses. They also enabled the comparison of the present and the earlier results. On the other hand, with only four channel recordings the results of the present experiment can not be discussed in terms of the detailed topography of visual cortex. It can only be assumed that each electrode recorded the activity of a broad "region of the cortex". With a typical head size, the distance between the adjacent electrodes was 7 cm. Using available theoretical data and the results of model testing (Niedermeyer and Lopes Da Silva 1993, Nunez 1981,) it was estimated that the cross-talk between electrodes should be less than 20%. With this accuracy each electrode recorded from its own region. Thus, the Oz electrode recorded from the primary visual cortex whereas the Pz electrode was positioned over the region of secondary and higher order visual fields in the parietal lobe. The Cz electrode was added to provide compatibility with other P300 studies. This electrode recorded the highest P300 waves. It probably recorded from the association cortex at the border of the visual region and from the regions involved in visuospatial at-

tention and memory (Corbetta et al. 1993). Finally, the Fz electrode recorded from the frontal cortex. Experiments on the visual system were attractive because the electrode montage typical for P300 studies also followed the dorsal stream of visual information processing. It is generally believed that the dorsal stream deals rather with spatial information processing whereas the ventral stream is involved in representation of objects (Ungerleider and Mishkin 1982). However, an integrated model of visual processing was recently suggested that emphasized the importance of information exchange between the streams. In particular, the close cooperation of parietal and occipital areas was suggested as a basic mechanism of an identification of visual objects (Bullier 2001). A number of experiments indicated the involvement of dorsal cortical areas also in pattern processing. Functional magnetic resonance studies of monkey cortex revealed shape specific activation in the intraparietal sulcus and the frontal eye field (Serenio et al. 2002). Electrophysiological studies also demonstrated shape selectivity in the intraparietal sulcus and the anterior intraparietal area especially if monkeys were trained to grasp real objects (Murata et al. 2000). Another electrophysiological study found shape selective neurons in the parietal cortex even when monkeys were fixating simple two-dimensional shapes (Serenio and Maunsell 1998). The shape selective responses in the dorsal areas may be used for grasping objects or for defining goals for eye-movements. However, since the shape selectivity persists independent of these functions it is probably also important in the other functions, perhaps in object recognition.

The largest components in probe responses were identified as the P200 waves. Previous experiments (Simson et al. 1976) showed the maximum amplitudes of this component over the primary visual cortex and again over the parietal region. Such result indicated that the P200 component was re-generated in these cortical areas. The probe responses in the frontal fields could not be volume conducted because their amplitudes in Fz were higher than in the Cz and Pz recordings. Moreover, the effect of P300 waves on probe responses was not the same in the different recordings. In particular, in the Fz recordings the probe responses following important stimuli were delayed rather than inhibited. The effect was probably genuine since it has also been observed in the earlier experiments (Michalski 2001).

The results of the present experiment indicate that the advent of an important stimulus reduces the effect of

noise. The effect of noise was significant only in responses to probes presented after the non-targets but not in responses to probes that followed the target stimuli. Moreover, the effect of noise was insignificant in responses to probes presented with the short delay after "odd-ball" stimuli (where interactions with P300 could be expected) but it became significant in responses to probes presented with the long delay. Such a result agrees well with Elbert and Rockstroh's suggestion that the "irrelevant" cortical activity evoked by noise should be inhibited after the advent of an important stimulus.

The separate analysis of data from each electrode revealed an interesting pattern of regular transition from sensitivity to noise stimulation to the sensitivity to stimulus relevance while moving from occipital to frontal recordings: (i) in Oz recordings, the noise reduced probe responses but the target stimuli were ineffective; (ii) in Pz recordings, both the target stimuli and the noise reduced probe responses; (iii) in Cz recordings, the target stimuli reduced probe responses but the noise was ineffective; (iv) in Fz recordings, neither the noise nor the target stimuli affected probe responses.

Such a regular pattern supports the prediction that the noise should affect mostly primary cortical areas and should be "filtered out" at higher cortical levels. On the other hand, a "higher activity" such as the evaluation of stimulus relevance should affect higher order cortical areas. It should be noted that this prediction is based on the hierarchical model of the visual system that has recently been challenged. The hierarchical model assumes that cortical processing starts in the primary visual area and that the subsequent stages of processing are performed in the secondary and higher fields. It was recently suggested however, that processing can start simultaneously or even earlier in the parietal than in the occipital cortex (Bullier 2001). Interestingly, in the present experiment the effect of noise was significant in Oz and Pz recordings but not in Cz and Fz recordings. The effects of noise on the early responses revealed a similar pattern: the reduction of these responses was highly significant in the occipital and parietal recordings, just significant in the central and insignificant in the frontal recordings.

The general inhibitory effect of noise on both the early responses and the responses to probes is in keeping with the results of single neuron recordings in animals. The inhibitory effect of large field stimulation with patterns consisting of short pieces of bars or gratings on the classic neuronal responses was reported in cat's cortical

area 17 and monkey's area V1 (Blakemore and Tobin 1972, Born and Tootell 1991, DeAngelis et al. 1994, Li and Li 1994, Orban et al. 1979, Sengpiel et al. 1997). In the monkey's area V1, specific neuronal responses were inhibited by whole-field stimulation with arrays of randomly oriented short bars (Knierim and Van Essen 1992), random noise (Gulyas et al. 1987, Hammond and MacKay 1975, Squatrito et al. 1990) or moving random dot pattern (Allman et al. 1990). On the other hand, an excitatory effect of noise was also reported. It was found that a strong noise background could facilitate responses to weak, subthreshold stimuli by producing the stochastic resonance effect (Wiesenfeld and Moss 1995). This effect was demonstrated in crayfish mechanoreceptors but also in humans where the noise enhanced the subject's ability to detect subthreshold tactile stimulation (Collins et al. 1996). The stochastic resonance produces effects similar to lowering neuronal firing thresholds thus, in the cortex, it should increase the number of responding cells. The inhibitory effect of noise observed in cortical recordings could then be due to the activation of inhibitory intercortical connections. From the point of view of Elbert and Rockstroh hypothesis, such reduction of responses can also indicate the existence of regulatory mechanisms responding to the increased amount of cortical activity.

The lack of the effect of noise on P300 amplitude was in striking contrast to the behavior of the other components indicating the different nature of this wave. Such a result was in keeping with the earlier observations that the P300 component was very insensitive to the physical parameters of the evoking stimuli (Donchin 1981, Donchin et al. 1986a,b, Israel et al. 1980a,b, Kramer et al. 1987, Polich 1989). On the other hand, if the P300 wave originated from the inhibition of irrelevant activity, its larger amplitude could be expected simply because there was more to inhibit. The increased level of neuronal activity in response to noise stimulation could be expected from animal experiments. Whole-field stimulation with drifting random dots activated the majority of cells in striate cortex of anesthetized cat (Skottun et al. 1988). In cortical area V1 of the alert monkey, dynamic random dot pattern also increased the firing rate of a large number of neurons (Squatrito et al. 1990). The lack of noise effect on the P300 amplitudes does not directly contradict Elbert and Rockstroh's hypothesis. The inhibitory signal can be simply strong enough to silence the irrelevant neurons regardless to their initial activation. Alternatively, the total energy



carried by the P300 potential can be increased by elongating this potential rather than by increasing its amplitude. Such elongation (longer falling time) was observed in the present recordings, but the effect was not strong and it needs the confirmation in future experiments.

## CONCLUSIONS

The manipulation of cortical activation with a noise stimulus seems to provide an interesting insight into the putative mechanisms of regulation of cortical responsiveness by the "relevant" stimuli. The reduction of noise effect by target stimuli supports Elbert and Rockstroh's hypothesis that the advent of important information inhibits "irrelevant" cortical activity. However, the present data indicate that the mechanisms of the regulation of responsiveness are not the same in the different cortical fields. Also, the lack of an effect of noise on P300 amplitudes indicates that the strength of the inhibitory signal is not proportional to the amount of "irrelevant" activity in the cortex.

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