ERP CORRELATES OF SPATIOTEMPORAL REGULARITY IN VISION

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ABSTRACT

Spatiotemporal regularities in stimulus structure have been shown to influence visual target detection and discrimination. Here we investigate whether the influence of spatiotemporal regularity is associated with the modulation of early components (P1/N1) in Event-Related Potentials (ERP). Stimuli consisted of five horizontal bars (predictors) appearing successively towards the fovea followed by a target bar at fixation, and participants performed a key-press on target detection. Results showed that compared to the condition where five predictors were presented in a temporally regular but spatially randomised order, target detection-times were faster and contralateral N1 peak latencies were shorter when the predictors and the target were presented with spatial and temporal regularity. Both measures were most prolonged when only the target was presented. In this latter condition, an additional latency prolongation was observed for the P1 peak compared to the conditions where the target was preceded by the predictors. The latency shifts associated with early ERP components provides additional support for involvement of early visual processing stages in the coding of spatiotemporal regularities in humans.

Keywords: Spatiotemporal regularity, Event-related potentials, Visual cortex, Human

INTRODUCTION

The way in which objects appear and move in our visual environment is often predictable, reflecting a stream of events which are spatially and temporally coherent. This spatiotemporal regularity, along with other common regularities existing in our natural surroundings, is assumed to be informative for an efficient visual system in processing of visual inputs [1], and such inferential processes in vision have been evidenced by the modulation of both perceptual sensitivity and neural responses when processing scenes for which the visual system has prior knowledge or expectations [for reviews, see 1-3].

Using a stimulus sequence comprising four collinear bars (predictors) appearing successively towards the fovea, followed by a target bar with the same or different orientation, Guo *et al* [4] showed that human orientation judgement for the target bar was biased towards the orientation of the predictors. The degree of this bias was correlated to the spatiotemporal prior probability induced by the orientated predictors (i.e. stronger bias for the predictors presented in a highly ordered and predictable sequence, with less bias for the predictors presented in a randomized order or with randomized duration), suggesting that contextual information about this spatiotemporal regularity is integrally used in the reconstruction of the visual scene when processing local visual information.

Within our extensive cortical neural network connected with feed-forward, lateral and feed-backward connections [5], it is still unclear where and how this spatiotemporal regularity is computed. However, recent extracellular recordings from monkeys have suggested the involvement of primary visual cortex (area V1), the first cortical stage of visual processing [6-9]. When the predictors were consecutively presented in a highly ordered and predictable sequence towards a neuron’s classical

receptive field (CRF) with its preferred orientation, up to half of recorded V1 neurons responded to the predictors prior to and distant from stimulation of their CRFs, and some neurons' orientation tuning to the CRF target bar were systematically biased towards the orientation of the predictor bars [9]. This suggests that the computation of spatiotemporal regularity starts at the earliest stage of visual processing, and that those modulated early neuronal responses may be correlated with the modulation of human orientation perception demonstrated in psychophysical experiments [4].

Here we aim to extend this study of neural computation of spatiotemporal regularity to human observers. With its advantage of higher temporal resolution, scalp recording of Event-Related Potentials (ERP) was employed. We expect a modulation of early ERP measures (P1/N1 deflections) as a function of spatiotemporal regularities in the visual scene which may be linked with perceptual performance recorded at the same time. Such approach would be relevant for our future study examining to what degree human perceptual performance corresponds with underlying neural computation in processing visual signals in natural contexts.

METHOD

Participants: Ten volunteers participated in this experiment. All participants (mean age = 21; sd = 1.3) were right handed and had normal or corrected to normal vision. Informed consent was obtained from each participant, and all procedures complied with the British Psychological Society "Code of Ethics and Conduct".

Materials and procedure: Visual stimuli were generated using a ViSaGe graphics system (Cambridge Research Systems, UK) and displayed on a high-frequency non-interlaced gamma-corrected colour monitor (100 Hz frame rate, 1024×768 pixels, Mitsubishi Diamond Pro 2070SB) with a uniform grey background

(24 cd/m^2 luminance). They consisted of six horizontal short bars (1.5° length, 0.1° width, 15% contrast) which were presented collinearly and successively towards the centre of the screen marked by a small red fixation point (FP, 0.15° diameter, 7.8 cd/m^2 luminance). The first five bars were predictors and were presented away from FP, the sixth bar was the target and presented 1° below FP. Participants viewed the visual stimuli binocularly with their heads placed in a chinrest at a distance of 57 cm from the monitor in a quiet, dim-lit room. After a warning tone (350 Hz, 150 ms), the predictor-target sequences were drawn from three conditions, Predictable condition (Pr), Random condition (R) and Target alone condition (TA), in a randomized block design (Fig. 1). In Pr and R, the first predictor was presented 500 ms after the warning tone. Each bar was presented for 200 ms, followed by a 100 ms delay before presentation of the next bar. The target was always presented immediately below FP in all conditions. There was no spatial interval between the locations of the adjacent bars: In Pr, the locations of the five predictors followed a straight horizontal line from the most extreme left location (6.75° relative to fixation) to the target location below FP. Predictor bars in R were presented at the same predefined predictor locations in the left visual field, but the order of the predictors' locations was randomized. In TA, only the target bar was presented, although the delay between the warning tone and onset of the target bar was kept the same as the time delay between warning tone and target presentation in Pr and R. Participants were instructed to maintain fixation during the task, to press a response key on the detection of the target bar, and to ignore any peripheral stimuli presented before the target. The experiment consisted of two blocks of 75 trials (in total 50 trials in each condition), which were presented after a short practice block consisting of 10 trials to allow familiarization with the task.

ERP-recording: EEG was recorded with a sampling rate of 256 Hz from 64 scalp locations using active Ag-AgCL-tipped electrodes attached to an electrode cap using the 10/20 labelling systems. The Active Two system (Biosemi, Amsterdam) was used for recording, which does not require gain adjustment or measurement of impedance. EEG signals were referenced during the recording to an additional active electrode (Common Mode Sense). In addition to the electrode cap, four electrodes were used to record electro-oculograms (EOGs). Two electrodes were placed at the outer canthi of both eyes (horizontal EOG) and two electrodes were placed on infraorbital and supraorbital locations of the right eye (Vertical EOG). Two additional electrodes (placed behind the left and right ear) were use for the off-line linked-mastoid referencing process. Signals were filtered off-line (high-pass filter: 0.1 Hz; low-pass filter: 70 Hz). Segments were time-locked to the onset of the first predictor bar and to the onset of the target bar by triggers sent to the recording system. Raw EEG was first segmented in epochs of 2400 ms (which included a 100 ms baseline). After rejection of trials with horizontal eye-movements and EOG correction for blink-artifacts, separate segments were created for the pre-target epoch (1500 ms, included a 100 ms baseline) and the target epoch (800 ms, including a 100 ms baseline), separately for the three experimental conditions. Segments with amplitude change greater than 180 uV or with amplitudes exceeding the amplitude criterion (± 100 uV) within 200 ms intervals at the scalp electrodes were rejected with an automatic rejection algorithm.

ERP-Analyses: Within the target epoch, the latency window for P1 (110–170ms) and N1 (170–235ms) was determined by visual inspection of the waveforms at the posterior electrode locations (PO7/PO8, PO3/PO4, and O1/O2). Peak latency for P1 and N1 was defined as the global maximum within each specified time-

windows (automatic peak detection). As peak-latencies for target P1 and N1 were different for the three testing conditions, P1/N1 peak-to-peak amplitudes were used for analysis. Following target N1, a difference between conditions was observable within the latency window 220-300 ms at posterior and occipital electrodes (analyzed at PO3/PO4) and was assumed to reflect the influence of the N2 on the averaged ERP signal. As peaks for this component were not clearly detectable, only mean amplitudes were analyzed.

Visual inspection of the pre-target waveforms revealed an increased negative drift from the onset of predictor two to target onset over the central and posterior electrode locations. This increased negativity between warning signal and response stimulus (Contingent Negative Variation: CNV) is generally associated with motor preparation and time-uncertainty [10]. To establish whether the ERP effects observed at posterior electrode locations occurred independently from the CNV, the raw data was filtered a second time with a higher high-pass filter (1 Hz) before repeating the analysis of ERP measures (first and second reported F and p-values in the Results section, respectively). For all analyses, the Greenhouse-Geisser adjustment was used whenever appropriate in the interpretation of statistical results. Only significant main effects are reported.

RESULTS

***Behavioural data*:** Response times to detect the target bar presented at fixation differed significantly across the three conditions [$F(2,18) = 43.48$; $p < 0.001$]. Pair-wise comparisons confirmed that mean response time to targets in Pr (251±7ms,

Mean±SEM) was faster compared to the R (295±9ms; $p < 0.001$) and TA (325±11ms; $p < 0.001$). Responses in TA were also significantly slower than in R ($p = 0.003$).

Peak-latency: P1 peak-latency analysis as a function of Hemisphere, electrode Site and Condition revealed a significant effect of Hemisphere [$F(1,9) = 9.02$ and 8.28; $p < 0.02$] (with shorter P1 peak-latencies over the left scalp), Condition [$F(2,18) = 11.17$ and 4.32; $p < 0.03$], Site [$F(2.18) = 10.58$ and 9.35; $p < 0.002$], and a significant interaction between Site x Hemisphere [$F(2,18) = 6.63$ and 6.378; $p < 0.007$] and Site x Condition [$F(4,36) = 5.56$ and 4.72; $p < 0.004$]. The effect of Condition was more pronounced over the right posterior scalp and was significant at PO3/4 [$F(2,18) > 10.5$ and 8.9; $p < 0.002$] and at O2 [$F(2,18) = 5.41$ and 4.03; $p < 0.04$]. At all three sites, P1 latency was significantly longer for TA compared to Pr ($p < 0.01$) and R ($p < 0.02$), but the difference between Pr and R was not significant (see Fig. 2). On average, P1 latency was 15 ms longer in TA compared to Pr and R. This site-specific effect of Condition resulted in a different time-course of peak-latency across the analyzed electrode: in TA, P1 peaked earlier at the more lateral electrode sites PO7/8 [$F(2,18) > 3.7$ and 3.5; $p < 0.05$] compared to PO3/4 ($p < 0.02$) and O1/2 ($p < 0.04$). This effect of Site was not significant in Pr and R.

N1 peak-latency analysis revealed significant effects of Hemisphere [$F(1,9) = 5.43$ and 4.48; $p < 0.05$] (with shorter latencies over the left posterior scalp), Condition [$F(2,18) = 9.67$ and 4.38; $p < 0.05$], and a significant interaction between Site and Condition [$F(4,36) = 6.12$ and 5.56; $p < 0.03$]. The effect of Condition was significant at PO3/4 [$F(2,18) > 9.5$ and 4.3; $p < 0.03$] and O2 [$F(2,18) = 16.4$ and 9.03; $p < 0.002$]. At PO3, N1 latency was significantly faster for Pr compared to TA ($p < 0.023$), but not compared to R. At PO4 and O2 however, all comparisons between TA, Pr and R were significant ($p < 0.01$): N1 peak-latency for Pr was

significantly faster compared to R and TA (difference was on average 14 ms), and N1 peaked significantly faster for R than for TA (with a difference of 8 ms on average). The differential effect of Condition at the different electrode sites was also reflected in dissimilar time-courses of peak-latency across the analyzed electrodes: In TA, N1 peaked earlier at PO7/8 [$F(2,18) > 6.0$ and 4.4; $p < 0.03$] compared to PO3/4 ($p < 0.03$) and O1/2 ($p < 0.01$). In Pr and R however, P1 peaked earliest at PO3/4 compared to PO7/8 and 01/2, but this effect was only significant for Pr over the right scalp $F(2,18) = 4.01$ and 3.74; $p < 0.05$].

Amplitude: Analysis of P1/N1 peak-to-peak amplitude revealed a significant effect of Site [$F(2,18) = 11.4$ and 12.9; $p < 0.01$], and significant interaction effects between Condition x Hemisphere [$F(2,18) = 4.65$ and 4.7; $p = 0.023$] and Site and Condition [$F(4,36) = 4.42$ and 4.75; $p < 0.005$]. Further analyses revealed a significant effect of Site for Pr and R over the left and the right posterior scalp [$F(2,18) > 10.8$ and 9.9; $p < 0.003$], which was not significant in TA. Both in Pr and R, amplitude was greatest at PO7/8 (mean = 7 μV), intermediate at O1/2 (mean = 5.5 μV) and smallest at PO3/4 (mean = 4.5 μV): PO7/8 *vs.* PO3/4: $p < 0.005$; PO7/8 *vs.* O1/2: $p < 0.016$; O1/2 *vs.* PO3/4: $p < 0.05$. The effect of Condition was only significant over the right scalp, at PO4 [$F(2,28) = 9.76$ and 9.72; $p < 0.001$] and O2 [$F(2,18) = 3.76$ and 3.67; $p < 0.05$], where peak-to-peak amplitude was significantly enhanced in TA as compared to Pr and R ($p < 0.04$). Differences between R and Pr were not significant. Results of P1 and N1 analysis are discussed under ‘General Discussion’.

Analysis of mean amplitudes within N2 latency window revealed a significant effect of Condition [$F(2,18) = 6.7$ and 10.1; $p < 0.01$]. The negativity was less in TA compared to P ($p = 0.01$) and R ($p = 0.02$), whereas the difference between the latter two conditions was not significant. The posterior visual N2 has been associated with

stimulus discrimination and classification processes [12, 13]. As the enhanced negativity in the latency-window for N2 was comparable for Pr and R, the increase in amplitude in these conditions may be related to stimulus classification processes which may be required when the target is embedded within a sequence of visual events.

GENERAL DISCUSSION

The influence of spatiotemporal regularities on ERP measures associated with target processing was predominantly characterized by peak-latency shifts in early ERP components: Compared to the Target Alone condition, P1 peak-latency at PO4 and O2 (contralateral to the visual field where the predictors were presented) was faster when the target was embedded within a sequence of predictor bars, whereas N1 peak latency at these electrode sites was shorter when the stimulus structure was characterized by spatial and temporal regularities (Pr) as compared to only temporal regularity (R). This N1 peak-latency shift is consistent with the effect across the three conditions on target detection times, implying a close link between human perceptual performance and neural responses associated with the processing of spatiotemporal regularities as reflected in the ERP latency effect. The potential causal relationship between these two measurements is currently under investigation in our laboratory.

In contrast to latency, amplitude of early ERP components to the target was not differentially affected in the Predictable and Random conditions, although P1/N1 peak-to-peak amplitude was enhanced when the target was not preceded by the predictors. This amplitude effect may however, be related to potential surround suppression effects associated with processing of the preceding predictor bars. Using magnetoencephalography (MEG), Ohtani *et al* [14] found that the amplitude of early

visually evoked magnetic responses to the central test grating was suppressed in conditions where the test stimulus was surrounded by adjacent high-contrast gratings, even when stimulus-onset asynchrony between surround context and test stimulus was increased to 2000 ms. The variation in scalp distribution of amplitude in response to our different conditions may reflect a similar surround suppression effect: Over the right posterior scalp, where the effect of condition was most pronounced, amplitude was reduced at PO4 and O2 compared to PO8 in the predictable and random conditions, whereas amplitude did not vary across these electrodes in the Target Alone condition. It is important to note however, that the surround suppression effect observed in Ohtani et al's study [14] only altered the amplitude of the visually evoked magnetic responses without any change in the peak-latency. The early ERP latency effects associated with target processing are therefore not likely to be related to surround suppression effects in the random and predictable conditions.

The latency-shift at P1 and N1 indicates that speed of target processing is facilitated when the target is embedded within a stimulus sequence defined by temporal or spatiotemporal regularities. It has been established that the latency of early ERP components can be influenced by a range of stimulus parameters, such as stimulus contrast on P1 latency [15] and luminance on N1 latency [16], whereas latency of both components is modulated by the type of target used in visual search tasks [17]. P1 latency has further been found to decrease during development [17] and to increase in old age [18]. Potential influences of any of these factors on the early latency-shift are however not probable given the consistency in task requirements and stimulus parameters of the target across the three conditions used in our experiment. Furthermore, although P1 amplitude is modulated by spatial attention and arousal state [11, 19, 20], and N1 amplitude is influenced by spatial attention and stimulus

discrimination [19, 20], these effects are generally reported without a change in latency. In a recent study, Doherty *et al* [21] further varied spatiotemporal stimulus structures to manipulate participants' expectation of possible locations for target presentation. Although P1 and N1 amplitude was modulated by spatial and/or temporal attention in their study, no P1 or N1 latency effects were reported beside a lateralization effect (shorter P1 latencies over the scalp contralateral to the visual field where the target appeared). Given these findings, the latency-shift found here is more likely to reflect influences of spatiotemporal regularity on visual target processing that occur independently from the established effect of attention on P1 and N1 amplitude. The effect may instead be exclusively associated with the influence of spatiotemporal prediction at early visual processing stages in situations where the target stimulus is embedded within a coherent sequence of visual events.

Spatial resolution limitations of the ERP method make it difficult to associate the latency-shift with specific neural sources. Although it has been noted that a large number of different visual areas are activated within the first hundred milliseconds after onset of a visual stimulus [22], results of dipole modelling in combination with PET have identified neural generator sources for the P1 wave beyond the striate cortex, in ventral and occipital regions [23], and potential neural generators for the N1 wave were found in the inferior occipital lobe and the occipitotemporal junction with converging imaging methods [24]. Our neurophysiological evidence suggests involvement of V1 in the coding of spatiotemporal stimulus regularities [9], but the relationship between these findings and the P1 and N1 latency-shift remains to be established. The timing of the peak-latency differences between predictable and random sequences (170-235) suggests that this latency-shift is likely the result of feed-backward processes. To establish if influences of regularity in stimulus structure

can be revealed within earlier ERP wave time-windows, the methodology could be modified to reveal the C1 wave (60 – 80 ms), which is assumed to be generated in area V1 [23].

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LEGENDS

Figure 1: Sequence of trial-events as a function of time (milliseconds) and condition (Predictable, Random and Target Alone conditions).

Figure 2: Average ERP waveforms for the Predictable, Random and Target Alone condition elicited by the Target bars at PO7/8, PO3/4, and O1/2.

Figure 1

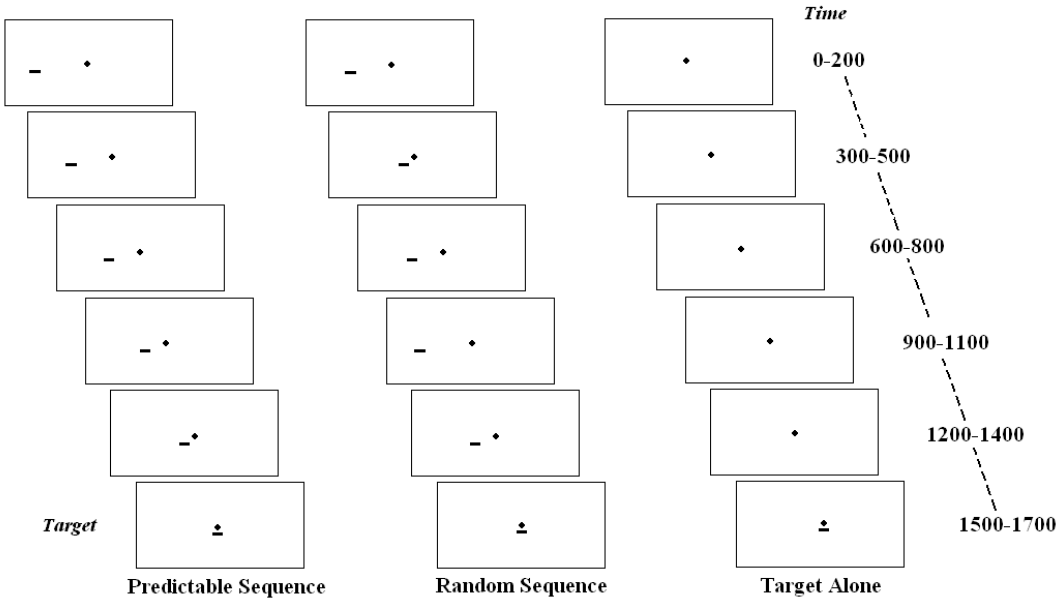
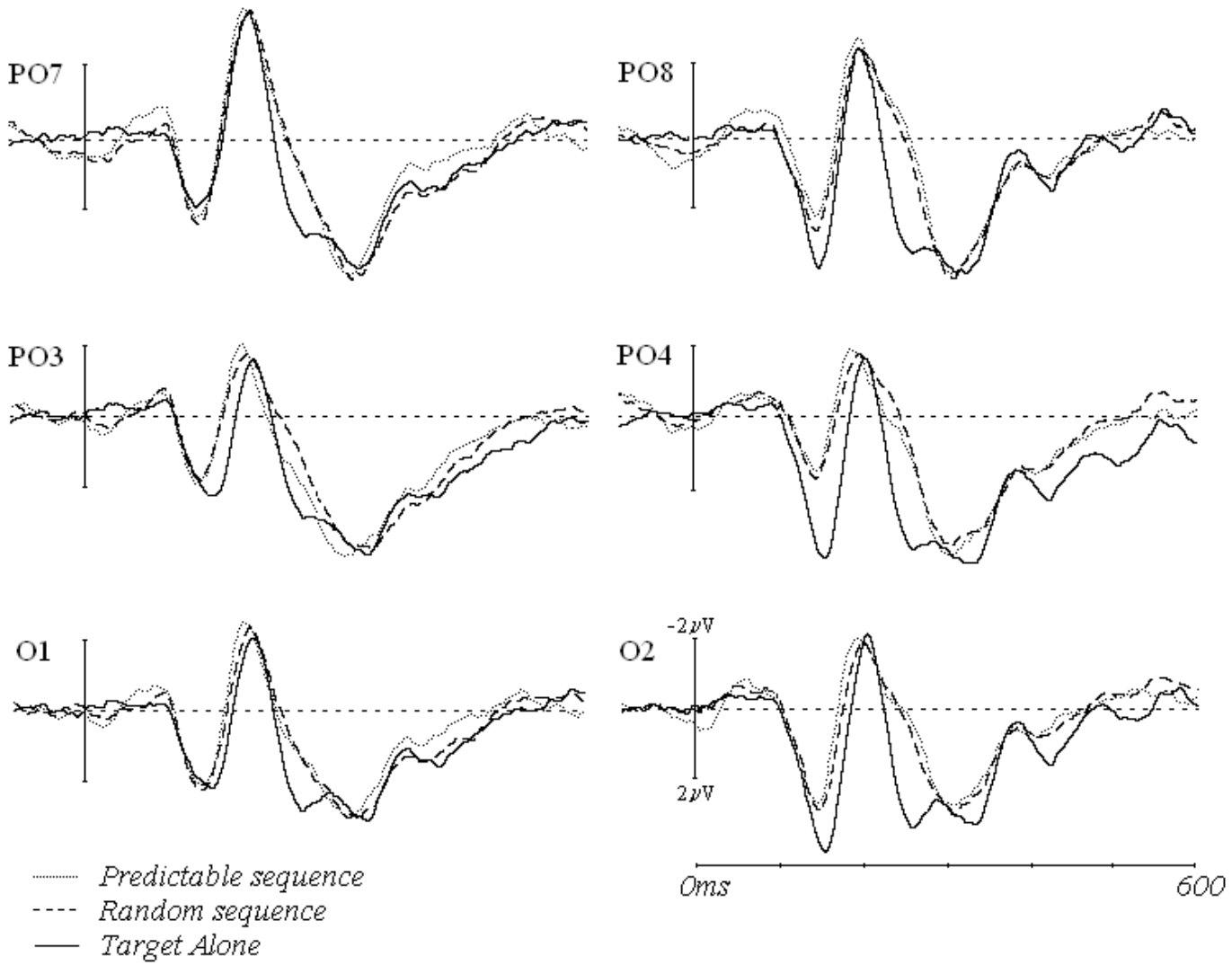

Time
0-200
300-500
600-800
900-1100
1200-1400
1500-1700
Target
Predictable Sequence
Random Sequence
Target Alone

Figure 2


PO7
PO8
PO3
PO4
O1
O2
-2μV
2μV
0ms
600
Predictable sequence
Random sequence
Target Alone