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Research Report

Differences in processing violations of sequential and feature regularities as revealed by visual event-related brain potentials

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A R T I C L E   I N F O

A B S T R A C T

Identifying novel or unexpected events which violate predictions based on the regularities extracted from our environment is crucially important for adaptive behavior. However, the exact dynamics of processing such events is not well understood. Furthermore, it is not known in which degree the process of deviant detection differs across contexts and how much it depends on the characteristics of deviant events. This issue was addressed by the present study which used event-related potentials (ERPs) in order to investigate the dynamics of identifying two types of deviants presented within the same visual setting. These events violated expectations based on two different types of information contained within each trial, either temporal order of stimulus presentation (sequential deviant) or physical attributes shared by the majority of individual stimuli (feature deviant). The obtained results indicate a certain degree of similarity in detecting two deviant types which, when task-relevant, both elicited N2 and P3b event-related potential components. However, significant differences across different stages of their processing were also identified. First, only feature, but not sequential deviants elicited an N1 enhancement. Furthermore, N2 and P3b responses elicited by sequential and feature deviants differed in their latency and topography and, in case of P3b, amplitude. Taken together, these results suggest that the dynamics of detecting different types of deviants strongly depends on the specific characteristics of such events. Furthermore, the identified differences in the topography of N2 and P3b indicate distinct mechanisms underlying several stages of their processing.

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1.   Introduction

In order to efficiently function and successively adapt to the environment one lives in, it is crucially important to learn about one's surroundings and capture their regularities occurring across different temporal and spatial scales. Such knowledge is useful as it allows one not only to efficiently process current information and make decisions in the present time, but also to plan and prepare for future events. The importance of such orientation towards the future expressed through the constant formulation and subsequent testing of one's expectations has recently been greatly emphasized (Bar, 2007; Butz et al., 2003; Schacter et al., 2007). The process of testing the validity of preformulated expectations by comparing these to the realized events can have two different outcomes. First, expectations may be formulated correctly in which case they are confirmed by incoming events. Although important, these events have somewhat limited informative value, as they primarily confirm a successful learning process. On the other hand, cases in which events occurring in the environment do not match the postulated predictions can be extremely relevant as they indicate that the learning itself was not successful or that something changed in the surroundings. Therefore, registering and further processing events which deviate from predictions is important, even in situations when they subsequently turn out to be irrelevant for the current goal or task at hand. Deviants which are later evaluated as relevant and informative can trigger an update of one's knowledge represented by internal models (Winkler et al., 1996; Winkler and Czigler, 1998) and a subsequent adaptive behavioral modification. In contrast, the irrelevant ones can be ignored, allowing the individual to reorient himself to the task at hand (Corbetta et al., 2002; Escera et al., 2000). Such potential significance of deviant events on cognitive processing and behavior is reflected on the level of our nervous system which is highly sensitive to novel events, changes in the environment and other types of errors in prediction (Corbetta and Shulman, 2002; Friston et al., 2006).

Deviant detection or the effects of violating predictions have previously been studied in many different contexts: e.g., active and passive oddball paradigms within different perceptual modalities as well as tasks addressing violations of temporal, language, music and sequential structure. The process of detecting violations exhibits a certain degree of similarity across different types of paradigms and cognitive domains. For example, it is electrophysiologically often characterized by a negative event-related potential component peaking around 200 ms, e.g., the mismatch negativity (MMN) or N2b in auditory and visual processing (Näätänen et al., 2007; Patel and Azzam, 2005), the early left anterior negativity (ELAN) in language (Friederici et al., 1999; Hahne and Friederici, 1999) or the early right anterior negativity (ERAN) in music processing (Koelsch et al., 2000). This negativity is typically followed by a later positive component, e.g., P300 or P600 (Friederici et al., 1996; Linden, 2005; Polich, 2007). Some components identified across different domains may be closely related to each other which is indicated by similarities in their topographies, latencies or other features.

This is, for example, the case for ELAN, a component elicited by phrase structure violations in syntactic language processing (Hahne and Friederici, 1999) and ERAN, a component which reflects the processing of music syntax (Koelsch et al., 2001). On the other hand, processing deviants across different contexts also greatly varies depending on factors such as, e.g., cognitive domain and the sensory modality in which the deviant occurs (Koelsch et al., 2001; Linden et al., 1999; Strange et al., 2000), attentional involvement of the participant (Näätänen et al., 2005), the characteristics of the deviant or expectations being violated (Koester and Prinz, 2007; Krigolson and Holroyd, 2007) and other (Patel and Azzam, 2005).

A recently conducted event-related fMRI study which investigated the process of detecting two different types of deviant events in the visual domain (Bubic et al., 2009) reported significant differences in brain areas and networks underlying their processing. Specifically, this study compared the detection of sequential deviants presented within the serial prediction task (Schubotz, 1999) and non-sequential (feature) deviants presented within a context basically similar to the one investigated by the classical oddball paradigm (Sutton et al., 1965). The results obtained in this study indicated that the two deviant types elicited distinct patterns of activations: while the detection of sequential deviants was primarily supported by right-lateralized prefrontal and premotor cortices, feature deviants mainly elicited activations within the posterior temporal and parietal cortex. This dissociation suggested that the neural correlates of deviant detection strongly depend on the characteristics of deviants and the expectations they violate. First, sequential deviants violated the specific ordinal context or the temporal order of stimulus presentation. Although it may appear that such events primarily violated temporal expectancies formulated within the serial prediction task (Coull et al., 2000; Coull and Nobre, 2008), it is important to emphasize that the temporal structure of the trial itself was not violated by the presentation of sequential deviants. Therefore, temporal expectations might have been relevant in this context only in interaction with those pertaining to the identity of the incoming stimuli. Non-sequential deviants, on the other hand, violated expectations pertaining to a specific stimulus characteristic (feature, category or class) which were formulated based on the overall stimulus context which is not dependent on exact stimulus order. Keeping this distinction in mind, the terms sequential and feature deviant will be used when referring to the two deviant types which were also investigated within the present experiment.

The main goal of the present experiment was to directly compare the temporal courses of processing sequential and feature deviants. This was done using a paradigm which was adapted from the one used in the described fMRI study (Bubic et al., 2009) and thus employed highly comparable experimental procedure, tasks and stimuli. In the course of this experiment, the participants were presented with trials composed of nine successively presented stimuli. These were organized in such a way that the first three stimuli constituted a sequential pattern which was later repeated twice. In some trials the last repetition of the pattern was incorrect and included a reversal in the order of two stimuli,

constituting a sequential deviant. Occasional individual stimuli which differed from the majority of stimuli in one feature, namely the color of their fixation cross, constituted feature deviants. In half of the trials participants were engaged in the sequencing (serial prediction) task (Schubotz, 1999), requiring them to attend to the order of presented stimuli and monitor for the presence of sequential deviants. In the other half of the trials they attended to the physical properties of individual stimuli and monitored for the presence of occasional feature deviants, thus being engaged in a feature (target detection) task (Fig. 1).

We hypothesized that the presentation of task-relevant deviant events in both task contexts would, in line with previously described event-related potential (ERP) components commonly associated with deviant detection across different contexts, be indexed by an early negative (N2-like) and a late positive (P3-like) response. Importantly, we hypothesized that the processing of the two deviant types should also dissociate, which could be reflected in different topographies of the identified event-related components. Specifically, corresponding to the findings from the previously described fMRI study (Bubic et al., 2009), more anterior and right-lateralized topography of components elicited by sequential deviants was expected. In addition, since the deviants could occur not only in the attended (task-relevant) but also non-attended (task-irrelevant) dimension of the stimuli, the current paradigm allowed us to address the relevance of attentional involvement in detecting both types of deviants. In relation to this question, we assumed that task-irrelevant sequential deviants may not elicit any specific responses, as it was previously argued that directing attention towards the sequential structure may constitute a necessary prerequisite for perceptual sequence processing (Schubotz and von Cramon, 2002).

2. Results

2.1. Behavioral performance

Behavioral performance was assessed by group average error rates which were 5.15% in the sequencing task and 6.85% in the feature task. A paired, two-tailed t-test used for comparison of performance in the two tasks revealed no significant difference ($t(13)=1.02$, $p=0.33$). Given that the participants' responses were delayed and occurred at different time periods following the critical event in the trial, response times were not used as an additional measure of behavioral performance.

2.2. Electrophysiological data

Standard, deviant, and deviant-minus-standard difference waves over Cz and Pz were formed separately per task and deviant type (Fig. 2). Difference wave amplitudes were tested against zero in one-sample, two-tailed t-tests over Cz (N1, N2), and Pz (P3), respectively. Task-relevant sequential deviants elicited significant N2 over Cz ($t(13)=2.238$, $p=0.043$) and P3 over Pz ($t(13)=5.284$, $p<0.001$). Task-irrelevant sequential deviants elicited significant N2 over Cz ($t(13)=2.388$, $p=0.033$),
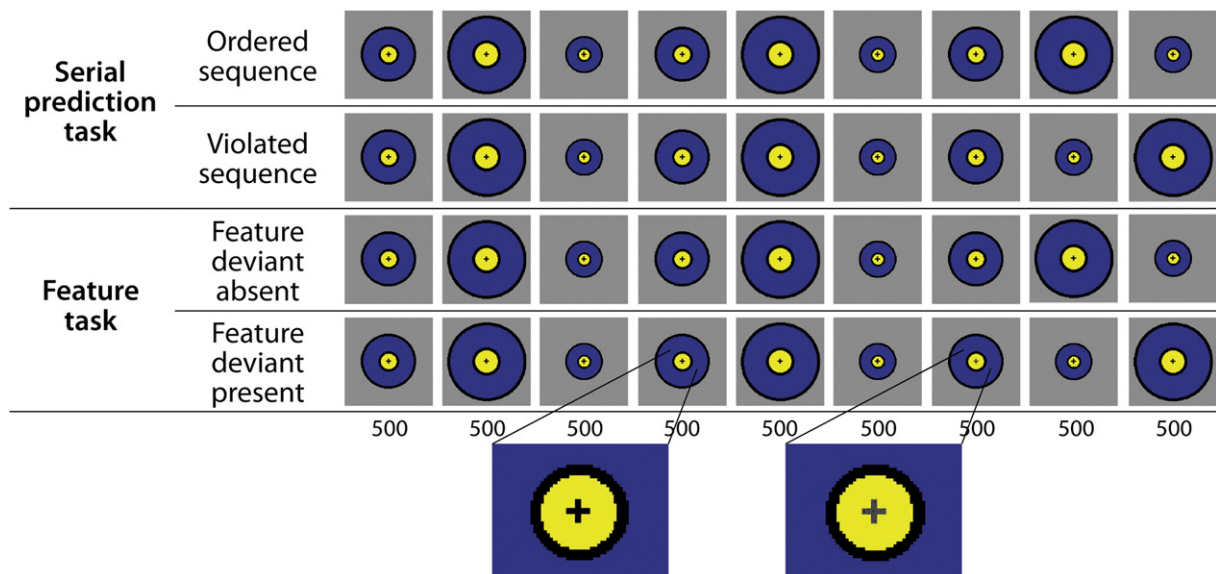

Fig. 1 – Schematic examples of four types of trials. Each trial included the presentation of nine stimuli, all presented successively with a duration of 500 ms and without a temporal gap. In ordered sequence trials the first three stimuli formed a sequential pattern which was then correctly repeated twice. Violated sequence trials also started with the 3-stimulus pattern which was followed by one repetition and one sequential deviant (here reversed order of 2nd and 3rd stimulus of the original pattern). Majority of stimuli within the experiment were feature standards (here highlighted in the 4th position of the last row), namely circles with a black fixation cross. Occasionally, feature deviants with a gray fixation cross were presented (here highlighted in the 7th position in the last row). During the two experimental blocks participants monitored for the occurrence of either sequential or feature deviants and always responded at the end of the trial.
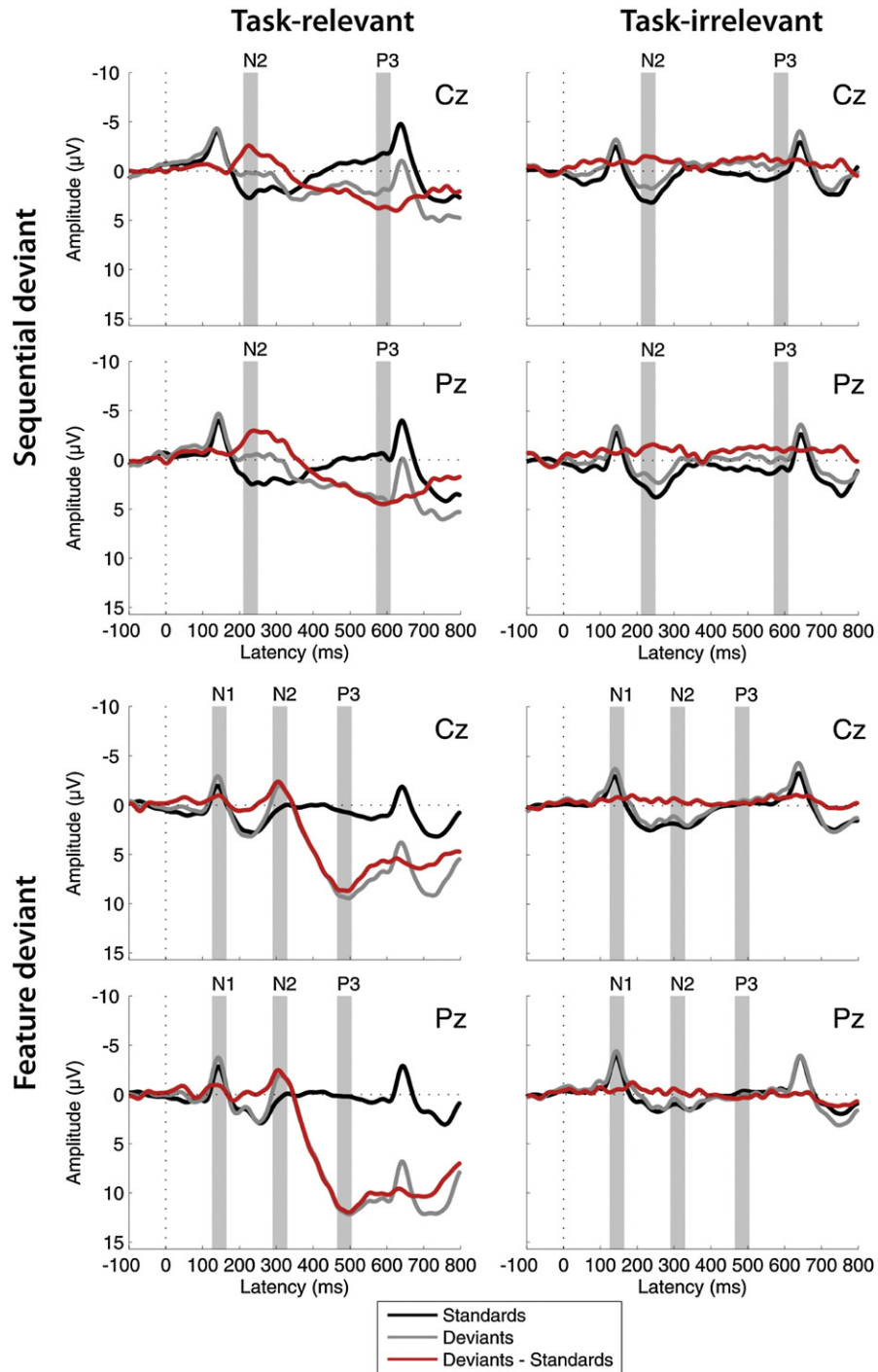
Fig. 2 – Event-related potentials (waveforms and difference waves) elicited by the presentation of standard and deviant stimuli in the two tasks presented in the experiment.

but not P3 over Pz ($t(13)=1.377$, $p=0.192$). *Post-hoc* analyses revealed that the N2 was elicited by task-irrelevant sequential deviants only in those participants who had first completed the sequencing task (participants who first completed the sequencing task: $t(6)=2.7284$, $p=0.034$; participants who first completed the feature task: $t(6)=0.63986$, $p=0.54591$). Task-relevant feature deviants elicited a significant N1-enhancement ($t(13)=2.163$, $p=0.0497$) as well as N2 ($t(13)=2.452$, $p=0.029$) and P3 ($t(13)=8.340$, $p<0.001$) components. For task-

irrelevant feature deviants, no significant activation was observed in the relevant component windows (N1: $t(13)=1.710$, $p=0.111$; N2: $t(13)=0.800$, $p=0.438$; P3: $t(13)=0.763$, $p=0.459$).

A comparison of components elicited by task-relevant sequential vs. task-relevant feature deviants which was conducted using paired, two-tailed t-tests showed no amplitude difference in N2 over Cz (sequential: -2.27 ± 1.01 μV, feature -1.98 ± 0.81 μV; $t(13)=0.225$, $p=0.825$), but a significant

amplitude difference in P3 over Pz (sequential: 4.44±0.84 μV, feature 11.74±1.41 μV; $t(13)=5.144$, $p<0.001$). Furthermore, significant latency differences in N2 over Cz (sequential: 228.9 ms, feature 308.6 ms; $t(13)=12.04$, $p<0.001$) and in P3 over Pz (sequential: 595.7 ms, feature 500.4 ms; $t(13)=4.47$, $p<0.001$) were observed. An analysis of topography differences for N2 and P3 components for task-relevant sequential and feature deviants was conducted using an analysis of variance (ANOVA) including the factors Deviant type (sequential/feature), Frontality (anterior/central/posterior), and Laterality (left/center/right). For both N2 and P3 the obtained results showed significant main effects of Frontality (N2: $F(2,26)=$ 12.29, $p=0.002$, $\varepsilon=0.61$; P3: $F(2,26)=26.57$, $p<0.001$, $\varepsilon=0.56$) and Laterality (N2: $F(2,26)=6.10$, $p=0.007$; P3: $F(2,26)=17.55$, $p<0.001$, $\varepsilon=0.67$) while factor Deviant type was significant only for P3 ($F(1,13)=19.44$, $p=0.001$). Furthermore, significant effects of interaction between factors Deviant type and Frontality (N2: $F(2,26)=7.19$, $p=0.012$, $\varepsilon=0.64$; P3: $F(2,26)=$ 15.71, $p=0.001$, $\varepsilon=0.59$), Deviant type and Laterality (N2: $F(2,26)=4.65$, $p=0.019$; P3: $F(2,26)=3.62$, $p=0.041$), and, in case of P3, interaction between factors Deviant type, Frontality and Laterality ($F(4,52)=3.18$, $p=0.043$, $\varepsilon=0.65$) were identified. Given that the amplitude of the P3 elicited by sequential and

feature deviants mutually differed, these topography differences were verified after normalizing the data using vector-scaling normalization (McCarthy and Wood, 1985). The obtained results showed a significant main effects of the factors Frontality ($F(2,26)=16.97$, $p<0.001$, $\varepsilon=0.54$) and Laterality ($F(2,26)=15.18$, $p<0.001$, $\varepsilon=0.71$) as well as the interaction between factors Deviant type and Laterality ($F(2,26)=4.64$, $p=0.028$, $\varepsilon=0.81$) (Fig. 3).

3.   Discussion

The present study explored the time course of detecting two different types of deviant events in the visual modality, namely those violating predictions related either to the sequential structure defined by the stimulus order (sequential deviants) or to physical features of individual stimuli (feature deviants). ERPs elicited by sequential and feature deviants were directly compared, revealing a dissociation between the two processes. When task-relevant, both types of deviants elicited N2 and P3 components of different latency and topography as well as, in case of the P3, amplitude. In addition, presentation of feature deviants elicited an enhancement of
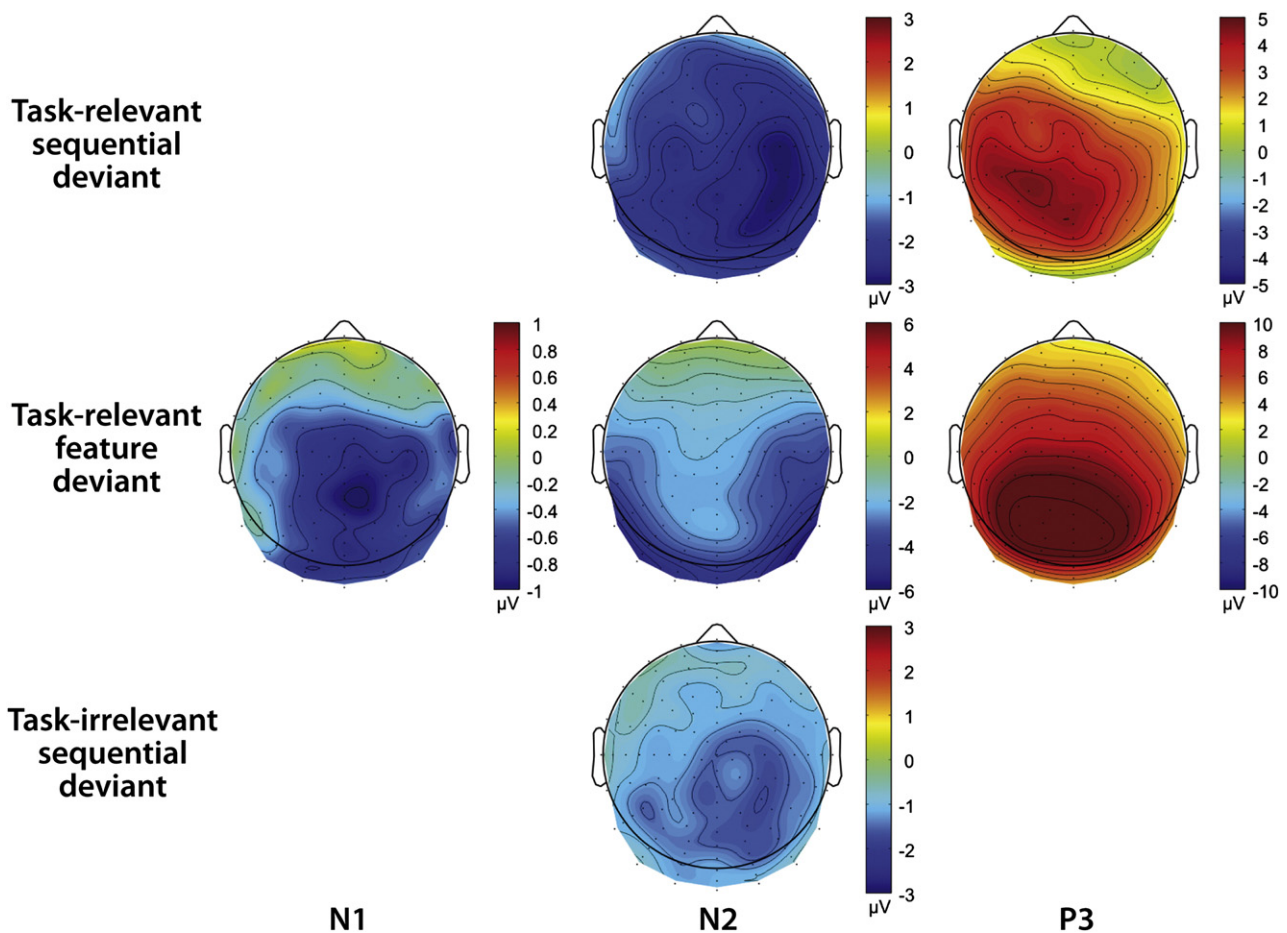

Fig. 3 – Voltage distributions for the ERP components elicited by task-relevant sequential deviants within the 210–250 ms (N2) and 570–610 ms (P3) time windows, task-relevant feature deviants within the 125–165 ms (N1), 290–330 ms (N2) and 465–505 ms (P3) time windows and task-irrelevant sequential deviant within 210–250 ms (N2) time window. Note the different scales for each component.

the N1 component. When task-irrelevant, sequential deviants elicited an N2 component which was present only in those participants who may have, due to the order of experimental sessions, been aware of the existence of the ordered sequential structure within the trials.

3.1. Similarities in detecting task-relevant deviants in the two task contexts

The results of the present experiment indicate that task-relevant, sequential as well as feature, visual deviants elicited a negative component peaking between 250 and 350 ms (N2) followed by a later positive component which peaked between 500 and 600 ms (P3). This pattern of results is in line with findings showing that the presentation of deviants within, e.g., the oddball task, elicits mainly the following components: N2, an early negative component occurring around 200 ms post-stimulus which has previously been related to the process of matching the stimuli to an internally generated, contextually appropriate template (Gehring et al., 1992) and P3, a later positive component occurring 300 ms after stimulus presentation which is typically suggested to reflect an update of the mental model of the environment required for making the appropriate response (Linden, 2005; Polich, 2007). The exact topography, latency as well as neural generators of these components identified within different task contexts depend on specific task requirements, most importantly the level of participants' attentional involvement in detecting such deviant events (Patel and Azzam, 2005). In the present study, the negative component elicited for both types of task-relevant deviants may reflect N2b, a negativity of central cortical distribution which is typically elicited by attended deviants in the oddball task where it is suggested to reflect voluntary processing elicited by a template mismatch or a deviation from expectation regarding the standard (Patel and Azzam, 2005). Since N2b has previously also been identified in other task contexts including stimulus and motor sequencing (Ferdinand et al., 2008; Rüsseler et al., 2003b), it is plausible to suggest that it signals controlled registration and classification of a deviant event across different task contexts (Novak et al., 1990). However, as will be described in more detail later, a very posterior distribution of the N2 elicited by feature deviants may likely correspond to the posterior modality-specific N2 component typically elicited in the oddball paradigm which may share some commonalities with other posterior negativities occurring in the N2 time range, such as the selection negativity or N2pc (cf. Folstein and Van Petten, 2008). In addition to this component, both feature and sequential deviants in the present experiment elicited P3, a positive deflection in an ERP waveform which reflects processing related to post-categorization evaluation of the stimulus and is mostly independent from response selection and execution (Coles et al., 1995). Given its features and the context within which it was identified (Patel and Azzam, 2005; Soltani and Knight, 2000), this component is suggested to represent P3b, an ERP response which reflects the updating of the underlying model of the event (Polich, 2007), context closure (Verleger, 1988) or post-categorization decision-related processing (Nieuwenhuis et al., 2005; Verleger, 2008).

3.2. Differences in detecting task-relevant deviants in the two task contexts

Although task-relevant feature and sequential deviants in the present study elicited similar ERP components, substantial differences in their latency, topography and, in case of P3b, amplitude, were revealed. However, a difference between the two deviant types was revealed even in an earlier processing stage. Specifically, only the appearance of feature deviants elicited an enhancement of N1, an early negative component which peaked after 100 ms following stimulus presentation. N1 represents a modality-specific component which has been suggested to reflect differential activations of feature-sensitive neural elements (e.g., Horvath et al., 2008). It is widely accepted in the auditory modality that N1 differences may be attributed to sensory adaptation implying a reduction of N1 for repetitive standard events (Näätänen et al., 1978; Näätänen and Picton, 1987; Näätänen et al., 2005). Similarly, it has been shown that early phases of detecting changes in the visual modality are influenced by differential refractoriness (Kenemans et al., 2003; Kimura et al., 2009). Although these findings do not imply identical neural generators or even temporal course of sensory adaptation in the two modalities, they do indicate functional similarity of N1 in auditory and visual processing. Thus, in the present study the initial enhanced processing of feature deviants can be attributed to a change in physical characteristics of these events in contrast to standards which shared task-relevant physical features and were therefore processed in a slightly attenuated fashion. The absence of such N1 enhancement in case of sequential deviants was expected, given that this violation type was not signalled by a physical change amongst otherwise identical instances of a given stimulus feature. Alternatively, however, the obtained difference in the N1 component might also reflect task-differential top-down attentional modulation. Specifically, it may be possible to suggest that the participants allocated more attention to visual feature processing stages in the feature when compared to the sequencing task, resulting in an enhanced N1 reflecting such more pronounced feature processing.

In addition to this early difference, dissociations in detecting sequential and feature deviants were also identified across later processing stages. Specifically, the two event-related components elicited by both task-relevant types of deviants, N2 and P3b, differed between the two conditions in terms of both latency and topography as well as, in case of P3b, amplitude. First of all, a shorter latency of N2 elicited by sequential deviants indicates that the comparison between expected and presented stimuli occurred earlier in this task context, resulting in a somewhat faster registration of the mismatch. This is interesting as the N1 effect in the feature condition shows that deviant information has already been registered by the system at an earlier level. However, it seems that the processes at the N2 level do not immediately benefit from this N1 effect. The earlier comparison process in the sequencing condition might imply that the expectations based on the learned sequence were available sooner than those based on physical stimulus properties. Alternatively, it is possible that the expectations were simultaneously present in both contexts and that the identified difference in N2 latency

reflects differences in the arrival of stimulus attributes relevant for the comparison. It is, however, important to notice that both of these suggestions are based on an implicit assumption according to which deviants are detected through a comparison between presented stimuli and preformulated expectations (predictive account) and not a memory trace which could also signify a retrospective comparison. Since this issue was not directly addressed within the present study, neither one of the two alternative explanations can be excluded.

Interestingly, the N2 in the sequencing task was then followed by a P3b which occurred later when compared to the one identified in the feature task. Taking into account previous findings showing that latency of the P3 increases with increasing difficulty of the decision (Kutas et al., 1977) and the suggestion that it may be used as an indicator of "stimulus evaluation time" (Donchin and Coles, 1988), the delayed P3b elicited by sequential deviants indicates that the overall decision process was prolonged in this condition. This could, on the one hand, indicate more complexity within this processing stage which might include not just the binary decision required for making the correct response, but also a subsequent update and restructuring of the internal model representing a sequence as a whole. This alternative was, however, not tested and would need to be further addressed in future experiments. Alternatively, the longer latency of P3 can be related to the nature of sequential deviants which were defined based on the relationship (transition) between pairs of stimuli. In order to make a decision regarding the presence of a deviant, two stimuli needed to be presented and considered, potentially leading to a delayed decision. This would be reflected in an increased P3 latency in comparison to the one identified in the feature task. An indicator of this comes from participants' reports which were given during the post-experimental briefing. Specifically, some participants indeed focused on the mutual relations between the neighbouring stimuli and occasionally adopted the strategy of verifying the sequential deviation using two consequently presented stimuli. However, it is important to emphasize that this strategy was not employed by all participants. Other participants reported making their decision right after the presentation of the first stimulus of the violated pattern based on the memorized size of individual stimuli. Such strategy differences are relevant because they can influence the exact timing and confidence in the decision without increasing the overall task difficulty. Specifically, more variable strategies in the sequencing task could result in a more variable time of onset of the P3 response across participants. This could then be related to the identified smaller amplitude of the P3b elicited by sequential deviants in contrast to the one identified in case of feature deviants which was very pronounced and characterized by a sharp onset and offset. However, since strategies could differ not just across, but also within participants and across different trials or parts of the experiment, we were not able to systematically analyze their influence, leaving this question open to be addressed in future experiments.

In addition to the described differences in amplitude and latency, both N2 and P3b identified within the two conditions were also characterized by different topographies. Generally, such differences suggest that the neural generators underly-ing the components elicited by the two deviant types are not identical which is plausible if one takes into account their complex nature. For example, it has previously been shown that P3 is not a unitary component, but a response which reflects activity of widely distributed sources whose coupling may depend on the task context in hand (Johnson, 1986). Furthermore, this response can be separated into subcomponents characterized by different sensitivity to the sequence of preceding events (Jentzsch and Sommer, 2001). Keeping this complexity in mind, the topography differences identified within the present study probably reflect a separation in neural generators of the elicited components. Such a separation indicates the existence of pronounced differences in the mechanisms underlying the processing of sequential and feature deviants. A more posterior distribution seen for both N2 and P3b in case of feature deviants is in line with the dominantly posterior activation pattern identified in this context using fMRI (Bubic et al., 2009). Specifically, the topography of the N2 identified in the feature task in the present study was restricted to posterior regions which were sufficient for supporting the comparison of the expected and incoming stimuli and correctly classifying the deviants. This is in line with previous findings which have indicated the appearance of a posterior, occipito-temporal negativity elicited by rare visual targets in the oddball task which are typically interpreted as reflecting attentional involvement required by such events (Folstein and Van Petten, 2008). In contrast, more anterior distribution of N2 in the sequencing task can be interpreted by taking into account the fact that the process of matching predictions and incoming stimuli in this context was based on more complex relations of neighbouring stimuli. The representation of such sequence was suggested to reflect an internal (forward) model subserved by more anterior, parietal and premotor areas (Schubotz and von Cramon, 2003). If so, these areas could also be involved in comparing the postulated model with the incoming stimuli. Interestingly, previous findings have also indicated that the posterior N2 may be elicited by deviants characterized even by simple visual features, in contrast to more complex or highly unfamiliar ones which elicit a more anterior novelty N2 component (Folstein and Van Petten, 2008). Finally, the obtained differences in the topography of N2 in the two task contexts could be related to the identified differences in the latency of this component. Given that the comparison process was supported by different brain regions, it is plausible to assume that these performed the suggested processing in different points in time. In addition to N2, differences in P3b topography were also identified, potentially reflecting previously described differences in the decision-making process in the two contexts or the subsequent updating of the model, a process which may be more prominent in the sequencing task.

3.3. The importance of attentional involvement in detecting deviants in the two task contexts

In addition to investigating the processing of task-relevant sequential and feature deviants, the design of the present study allowed us to investigate whether task-irrelevant sequential and feature deviants are also registered and processed similarly to those presented in the attended, task-

relevant dimension or not. The obtained results show that task-irrelevant deviants, in contrast to the task-relevant ones, failed to evoke a strong response in either of the two task contexts. Interestingly, a negative component peaking after 200 ms was elicited only by task-irrelevant sequencing deviants, despite the fact that they, when task-relevant, elicited a P3 of longer latency and smaller amplitude when compared to the feature deviants. However, a *post-hoc* analysis indicated that this component was only present in those participants who had completed the sequencing task first. In this subgroup of participants, previous knowledge related to the existence of an ordered trial structure may have been transferred to the trials in which only physical features of individual stimuli needed to be monitored. Although not any more relevant, the knowledge about the sequential structure affected the participants' responses to the presented deviants. This influence is in line with findings showing that informing subjects about the task-irrelevant aspect of presented stimuli can influence their subsequent processing and performance (Mack et al., 1992). In contrast, participants who were completely naïve with respect to the sequential structure of the trial failed to register the existence of task-irrelevant sequential deviants. Therefore, in the absence of prior knowledge, attentional involvement appears to be necessary for detecting deviants in both task contexts, which indirectly suggests that it was also needed for learning the sequential structure within the trials. This is in line with the suggestion about the importance of attentional involvement in learning perceptual sequences within the sensorimotor forward model framework (Schubotz, 2007) and findings showing that explicit knowledge is more likely to be used for forming expectations about incoming stimuli (Willingham et al., 1989). In addition, these results pertain to the debate whether stimulus dependencies can be learned implicitly (Nattkemper and Prinz, 1997; Rüsseler and Rösler, 2000; Rüsseler et al., 2003a) and suggest that such implicit learning is possible, but dependent on participants' previous knowledge regarding the existence of such relations. However, even when present, implicit sequence learning is not equivalent to the one which occurred when the attention of participants was directed towards sequential structure. Specifically, when attending to the order of stimulus presentation, all participants were able to learn the sequential structure and explicitly apply the acquired knowledge for detecting occasionally presented deviants. In contrast, when attending to physical features of individual stimuli, participants did not explicitly use the knowledge regarding the sequential structure for registering sequential deviants, as indicated by the lack of a P3 response following the N2 ERP component. Furthermore, in the post-experimental briefing only one participant reported that he had occasionally noticed regularity in the order of presented stimuli while performing the feature task. Of course, this does not imply that such learning could not become more elaborate in situations in which some features of the task (e.g., stimulus modality, sequence length, number of sequence repetitions, stimulus dimension defining the sequence) would be changed. If yes, based on the present results it is not clear whether it would share the neural substrate identified in processing explicit perceptual sequences (Schubotz et al., 2008). Similar conclusions can be made for task-irrelevant

feature deviants. Although not detected in the present experiment, they might be able to elicit a more pronounced response in the context where the feature defining their deviance would be made more salient (for a general discussion about pre-attentive deviance detection cf. Czigler et al., 2007; Escera et al., 2000; Näätänen et al., 2005).

3.4.   Concluding remarks

Results of the present study indicate both similarities and differences in detecting events deviating from different types of standard contexts. When task-relevant, both sequential and feature deviants elicited N2 and P3b components which differed in their latencies, topographies and, in case of P3b, amplitude. In addition, a difference in an earlier stage of their processing was identified, indexed by the enhanced N1 component only in the case of feature deviants. Overall, these findings indicate a certain degree of similarity in the process of detecting sequential and feature deviants which may in both cases include setting expectations about the incoming events, matching them to the presented stimuli and, in case of a mismatch, elaborating the violation in order to reach a decision about the presence of a deviant. However, the temporal course as well as the brain networks involved in processing sequential and feature deviants differ significantly. This leads us to conclude that the temporal dynamics and neural implementation of deviant detection critically depend on the nature of the deviant and the expectations it violates.

4.   Experimental procedures

4.1.   Participants

Fourteen healthy volunteers (7 male, 2 left-handed, mean age 24.9 years) with normal or corrected-to-normal vision participated in the experiment. None were taking any medication that might affect the central nervous system. According to the Declaration of Helsinki, written informed consent was obtained from each participant prior to the beginning of the experiment.

4.2.   Procedure

Participants were seated in a sound-attenuated and electrically shielded chamber. A computer screen, visible through a glass pane, was placed outside the chamber at a distance of 100 cm. Sequences of visual stimuli were presented in the center of the screen. Participants were provided with a response keypad.

4.3.   Stimuli and tasks

The stimulus material consisted of 10 circles with diameters ranging from 0.6 to 2.8 degrees of visual angle with a fixation cross in the middle of the circle. Each trial included successive presentation of nine stimuli with a duration of 500 ms without temporal gaps, followed by a 1500 ms response period and a 500 ms inter-trial interval during which a fixation cross was displayed. The first three stimuli of each trial formed a sequential pattern which was then repeated twice. In ordered

sequence trials these repetitions were always completely correct, while violated sequence trials included one full repetition and one sequential deviant characterized by the reversed order of 1st and 2nd or 2nd and 3rd stimulus of the original pattern. Thus, within each trial, sequential deviants could occur in positions 7 or 8 with 25% probability each. As mentioned before, each stimulus contained a fixation cross colored either black which was the case for the majority of stimuli (feature standards) or gray (75% of the original black color) in case of feature deviants. Within each trial, feature deviants were presented in positions 3, 4, 5 or 6 with 5% probability each and in positions 7 or 8 with 15% probability each. Throughout the experiment, the probability of occurrence of both violations was 50%. All stimuli were presented centrally on the screen.

The occurrence of sequential and feature violations was counterbalanced within participants. Stimulation was randomized individually for each participant, and was presented twice in successive parts of the experiment during which participants completed two different tasks on the presented stimuli. In the sequencing (serial prediction) task they were instructed to attend to the order of stimulus presentation and judge the sequential correctness by indicating whether a sequential deviant was presented at the end of the trial or not. In the feature (target detection) task participants attended to physical features of individual stimuli and were required to indicate whether a feature deviant was presented within the trial or not. An example of each type of trial is shown in Fig. 1. In both tasks, participants responded by button presses with their left and right index fingers. The response was always given at the end of the trial, which was indicated by the appearance of a question mark. Button-response assignment was counterbalanced across participants. Participants' performance was evaluated at the end of each block when they received feedback about their accuracy (percentage of errors) and mean response time. For each task, participants completed five blocks comprised of 48 sequences. In total, 480 sequences were thus presented. With 6500 ms per sequence, the overall duration of an experimental session amounted to 52 min. After the experiment, the participants filled out a short questionnaire in which they described their subjective impressions of the two tasks and reported strategies used for solving each one of them.

4.4. Data recording and analysis

Participants' responses were recorded and response times (RTs) were measured relative to the onset of the question mark (indicating the response window). EEG was continuously recorded with Ag/AgCl active electrodes from 128 locations radially equidistant from Cz according to the ABC layout (http://www.biosemi.com/headcap.htm), which roughly corresponds to the 10–5 extension of the international 10–20 system (Oostenveld and Praamstra, 2001). Electrodes were mounted in a nylon cap. Additional electrodes were placed at the tip of the nose, which served as off-line reference, and at the left and right earlobes. Eye movements were monitored by electrodes placed above and below the right eye and lateral to the outer canthi of both eyes, which were bipolarized off-line to yield vertical and horizontal electroocular activity (EOG), respectively. EEG and

EOG signals were amplified by BioSemi Active-Two amplifiers, sampled at 512 Hz, and filtered off-line using a band-pass filter from 0.1 to 30 Hz. Channels with technical malfunction (1 per participant on average) were replaced by interpolating the data of the surrounding electrode sites (Perrin et al., 1989). For each stimulus, epochs of 900 ms duration including a 100 ms pre-stimulus baseline were averaged with reference to stimulus onset to form ERPs. Epochs with amplitude changes exceeding 100 μV in any channel were rejected from averaging. All stimuli in a sequence with an incorrect behavioral response were also excluded from ERP averaging. Following these exclusion criteria, 75% of the to-be-analyzed stimuli were retained on average.

Separately for each type of deviant (sequential/feature), records were sorted as a function of stimulus type (standard/deviant), position (1–9), and task-relevance as defined by task instruction which specified participants' attentional involvement (task-relevant/task-irrelevant). Stimuli were analyzed only when there was no previous deviant of the other type in the sequence. Deviance-related difference waves per deviant type (sequential/feature) and task-relevance (task-relevant/task-irrelevant) were formed by subtracting the ERPs elicited by standards from those elicited by deviants in corresponding positions (7–8 for sequential standards and deviants, 3–8 for feature standards and deviants). Average ERP amplitudes of the deviant-minus-standard difference waves per condition were measured in 40 ms intervals around the relevant grand-average peak. Measurements were taken over Cz and Pz and larger electrode clusters were formed for topography analysis (Fig. 4). Difference wave amplitudes were tested against zero in one-sample, two-tailed t-tests over Cz (N1, N2), and Pz (P3), respectively. The amplitudes of components elicited by the two deviant types were mutually compared using paired, two-tailed t-tests. An analysis of topography differences for the
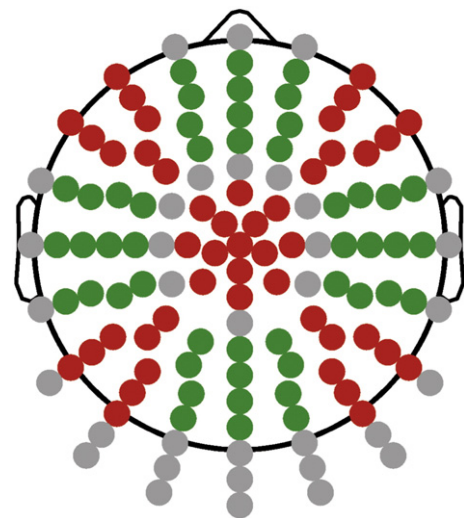

Fig. 4 – Layout of electrode positions. Electrodes colored gray were not chosen for the topography analysis, while those highlighted green and red represent nine different clusters which were analyzed with respect to the factors Frontality (anterior/central/posterior) and Laterality (left/center/right).

identified N2 and P3 components was conducted using an analysis of variance (ANOVA) including the factors Deviant type (sequential/feature), Frontality (anterior/central/posterior), and Laterality (left/center/right). In case amplitude differences in the components elicited by sequential and feature deviants appeared, the topography analysis was verified after normalizing the data using vector-scaling normalization (McCarthy and Wood, 1985). The Greenhouse–Geisser correction (Greenhouse and Geisser, 1959) was applied when the assumption of sphericity was violated. In addition, latencies of N2 and P3 elicited by the two deviant types were measured and compared using paired, two-tailed t-tests. Latencies were determined by applying the jackknife-based scoring method (Kiesel et al., 2008; Miller et al., 2009) on the component peak amplitudes.

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