Multimodal Effects of Local Context on Target Detection: Evidence from P3b

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Abstract

■ We used the P300 component to investigate how changes in local context influenced the ability to detect target stimuli. Local context was defined as the occurrence of a short predictive series of stimuli before delivery of a target event. EEG was recorded in 12 subjects during auditory and visual sessions. Stimuli were presented in the center of the auditory and visual field and consisted of 15% targets (1000 Hz tone or downward facing triangle) and 85% of equal amounts of three types of standards (1500, 2000, and 2500 Hz tones or triangles facing left, upward, and right). Recording blocks consisted of targets preceded by either randomized sequences of standards or by sequences including a three-standard predictive sequence signaling the occurrence of a subsequent target event. Subjects pressed a button in response to targets. Peak target P300 (P3b) amplitude and latency were evaluated for targets after predictive and nonpredictive sequences using conventional averaging and a novel single-trial analysis procedure. Reaction times were shorter for predictable targets than for nonpredicted targets. P3b latency was shorter for predicted targets than for nonpredictive targets, and there were no significant P3b amplitude differences between predicted and random targets, as determined by both conventional averaging and single-trial analysis. Comparable effects on amplitude and latency were observed in both the auditory and visual modalities. The results indicate that local context has differential effects on P3b amplitude and latency, and exerts modality-independent effects on cognitive processing. ■

INTRODUCTION

We rapidly and fluidly extract and utilize information from our environment to guide goal-oriented behavior and to facilitate the detection of task-relevant stimuli. The use of relevant information to guide our behavior allows one to mediate appropriate behavioral responses as a function of local context. However, the neural mechanisms underlying this mental process are not well understood.

Evidence from neuropsychological, event-related potential (ERP) and neuroimaging studies supports a key role of the lateral prefrontal cortex (LPFC) in contextual processing. Studies of patients with schizophrenia, showing an association of prefrontal dysfunction with impairment in context processing, suggests that this cortical area has a critical role in the processing of context (MacDonald et al., 2005; Barch et al., 2001). The proposition is that the LPFC recodes information into context representations (MacDonald, Cohen, Stenger, & Carter, 2000; Cohen & Servan-Schreiber, 1992). That is, information such as task instructions, a cue or the processing of preceding sequential stimuli, are maintained in the LPFC to facilitate appropriate response to target stimuli (Huettel, Song, & McCarthy, 2005; MacDonald et al., 2000; Cohen & Servan-Schreiber, 1992). Neuroimaging data from Huettel et al. (2005) have also reported that the LPFC has a critical role in the resolution of short-term uncertainty.

Electrophysiological studies also support a key role of the LPFC in contextual processing. For instance, contextual processing has been linked to the P300 component of the ERP (Polich & Criado, 2006; Poulsen, Luu, Davey, & Tucker, 2005; Donchin & Coles, 1988; Squires, Wickens, Squires, & Donchin, 1976). One hypothesis is that P300 generation reflects a process wherein a stimulus is evaluated in the context of the previous stimuli by comparing it with working memory content (Polich & Criado, 2006; Polich, 2003; Donchin & Coles, 1988). Other theories link P300 with such processes as cognitive closure, stimulus categorization (Verleger, 1988), and template matching (Chao, Nielsen-Bohlman, & Knight, 1995; Squires, Hillyard, & Lindsay, 1973). In the case of template matching, the closer the match of a stimulus to a template, the larger and earlier the P300 (Squires et al., 1973). ERP and neurophysiological data from neurological patients with LFPC damage also support a role of this brain region in contextual processing (Barcelo & Knight, 2007). These lesion-ERP findings in lateral frontal damage patients link the P300 family of ERPs to the guided activation model of frontal function (Barcelo & Knight, 2007; Miller & Cohen, 2001). The extant literature

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supports the notion that hypotheses about the environment are continuously generated as a function of incoming information (Donchin & Coles, 1988), and the P3b ERP component is associated with the evaluation of these as a function of context (Squires et al., 1976).

The target P300, known as the P3b, is elicited by the classical oddball target detection task, and has a posterior-parietal scalp distribution (Polich, 2003; Squires, Squires, & Hillyard, 1975). P3b latency is a measure of the timing of mental processes reflected by the component, whereas P3b amplitude has been proposed to reflect the intensity of these processes (Kok, 2001). P3b may be influenced by three main variables (Johnson, 1986): information transmission (equivocation and allocation of attention, also proposed to reflect resources invested in identification of a stimulus, Kok, 2001), subjective probability (affected by global probabilities and sequential expectancies), and stimulus meaning (a function of stimulus complexity, task complexity, and stimulus value). P3b amplitude and latency are affected by information transmission (reduced information transmitted by the stimulus results in smaller P3b amplitude and longer latency; Johnson, 1986; Sutton, Tueting, Zubin, & John, 1967; Sutton, Braren, Zubin, & John, 1965), global probability (higher global probability of a target stimulus results in smaller amplitude and shorter latency P3b; Polich & Bondurant, 1997; Johnson, 1986), sequential effects (P3b amplitude is larger and latency is shorter for targets preceded by a longer string of standards, compared to targets preceded by a short string of standards; Holm, Ranta-aho, Sallinen, Karjalainen, & Müller, 2006; Squires et al., 1976), and complexity of the stimulus (the more complex the stimulus, the larger the amplitude and the longer the latency of the P3b; Johnson, 1986; Kutas, McCarthy, & Donchin, 1977). P3b amplitude increases with increasing task complexity and increasing stimulus value or relevance to the task (Johnson, 1986; Wilikinson & Morlock, 1967). P3b amplitude is also affected by expectancy such that the less expected a stimulus is in the context of a sequential series of stimuli (i.e., if a repetitive pattern of stimuli is discontinued), the bigger the P3b amplitude (Polich & Bondurant, 1997; Johnson & Donchin, 1980; Squires et al., 1976). In addition, P3b amplitude has been shown to be suppressed in patients with prefrontal lesions (Barcelo & Knight, 2007; Barcelo, Suwazano, & Knight, 2000; Frodl-Bauch, Gallinat, Meisenzahl, Möller, & Hegerl, 1999; Alain, Hargrave, & Woods, 1988), supporting an important role of the prefrontal cortex in the modulation of the P3b component.

The aim of the present study was to use P3b ERP to examine the effects of a predictive sequence on local contextual processing. Experimentally, we modified the classical oddball target task such that instead of only one standard occurring there were equal amounts of three different standards as well as one designated target. This design allowed us to introduce a sequence that predicted subsequent targets, and to compare these to targets occurring randomly. We investigated the effects of local context by comparing predicted, random targets and the predictive sequence, to determine whether P3b amplitude increases as a function of the build-up of contextual information. Furthermore, we explored these effects in both the auditory and visual modalities to determine whether local context effects depended on the sensory modality. Methodologically, we extended the traditional ERP analysis method by incorporating single-trial analysis. Specifically, we used a novel technique called Analysis of Single-trial Event-related potentials and Ongoing activity (ASEO) to estimate P3b amplitude and latency of predicted and random targets on a single-trial basis in order to determine how these two parameters are affected by predictive local context.

METHODS

Subjects

Fourteen subjects (mean age = 25 years, 6 women) participated in the study. All the subjects were right-handed, had normal hearing and vision, and had no history of psychiatric or neurological problems. Subjects were consented prior to being tested and were paid for their participation. The Committee for the Protection of Human Subjects for University California, Berkeley, approved the study. Reliable recordings were obtained from 12 subjects in both the visual and auditory modality (in 2 of these subjects, the auditory sessions were excluded from further analysis; see below for details) and from another 2 subjects in the auditory modality only, such that overall, 12 recordings were obtained for each modality.

Task

Subjects sat in a sound-attenuated booth 110 cm in front of a 21-in. PC computer screen. Stimuli were presented in the visual and auditory modalities in two separate sessions. Stimuli consisted of 15% targets (1000 Hz tone or downward-facing triangle) and 85% of equal amounts of three types of standards (1500, 2000, and 2500 Hz tones at 65 dB SPL, with 9 msec rise time or triangles facing left, upward, and right). In each block, a total of 127 stimuli (19 targets, 36 of each standard type) were presented each for 100 msec and ISI of 1 sec. Recording blocks consisted of targets preceded by either randomized sequences of standards or by sequences including a three-standard predictive sequence. Figure 1 illustrates an example of randomized and predicted sequences. Each block consisted of 10 different randomized sequences of standards (1–10 standards long) preceding the target and 8 sequences of standards (3–10 standards long) with a predictive sequence preceding the target

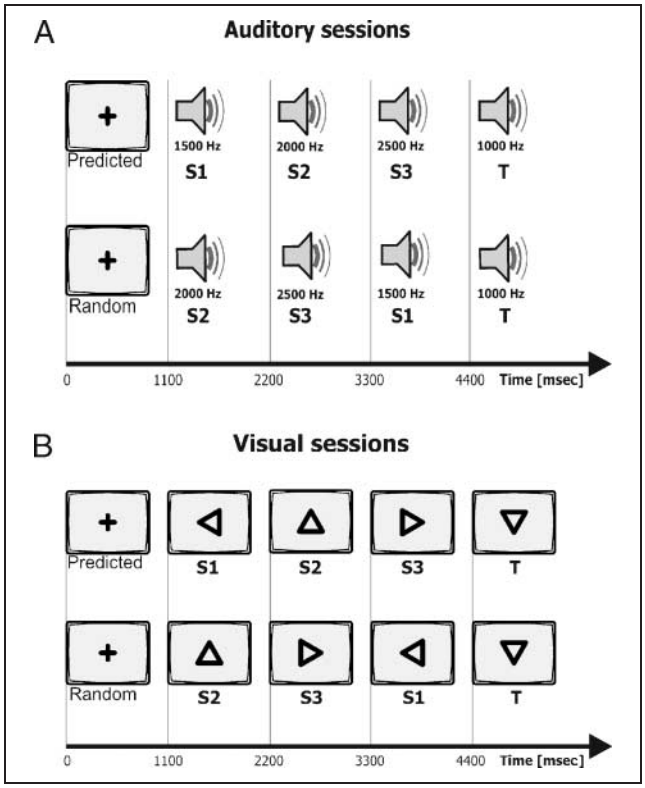

Figure 1. Auditory (A) and visual (B) sessions. Sequences of standards S1, S2, and S3 with a predicted sequence (top) and in randomized order (bottom) preceding the target (T). Stimuli presented centrally. Intertrial intervals, including duration of stimulus presentation (100 msec), are displayed.

in each. Visual stimuli were presented centrally on a computer screen and auditory stimuli from a central loudspeaker, both 110 cm in front of the subject. The subject was asked to centrally fixate throughout the recordings in both modality sessions. Each session in one of the modalities consisted of 12 different blocks, displayed in randomized order, each approximately 2.3 min long. Auditory and visual sessions were counterbalanced across subjects, such that the same number of subjects performed the auditory session followed by the visual session and vice versa.

Subjects performed a brief training session to ensure they were able to detect the target accurately. Subjects were then introduced to the predictive sequence before the recordings began and were aware that it would be 100% predictive of a target, but that targets would also appear randomly throughout the block. Subjects were asked to press a button each time a target was presented and to pay attention and look for the predictive sequence. Upon postscreening subjects who reported that they did not notice the sequence were excluded from analysis (two auditory sessions in two of the subjects). Stimulus presentation and response recordings were controlled using E-prime (Psychology Software Tools, Pittsburgh, PA).

Recording

EEG was recorded from 64 electrode array using the ActiveTwo system (Biosemi, The Netherlands). External electrodes above and below the right eye monitored vertical eye movements and electrodes placed laterally to the left and right eyes monitored horizontal eye movements. Linked ears were used as reference. Signals were amplified and digitized at 512 Hz and filtered at 0.16–100 Hz. Postprocessing and ERP analysis of the data was performed using Brain Vision Analyzer (Brain Products GmbH, Germany). All channels were re-referenced to averaged earlobes.

ERP Analysis

Prior to ERP analysis, ocular movements were defined using ICA and were removed by a linear derivation using Brain Vision Analyzer. Epochs containing misses (no button press 100–1100 msec poststimulus onset) were excluded from further analysis. EEG signals were filtered at 0.5–30 Hz for subsequent analysis. EEG signals were sorted and averaged relative to the stimulus onset, with epochs set from −100 to 1000 msec relative to stimulus onset. EEG epochs with amplitude of more than 75 μV at any electrode were excluded.

P3b was determined as the most positive point in the latency range of 200–700 msec in the auditory modality and 250–700 msec in the visual modality. N1 was determined as the most negative peak in the latency range of 50–200 msec.

Peak P3b amplitude (measured in microvolts) and latencies (measured in milliseconds) at Pz were evaluated for six conditions: targets after predictive sequences (predicted), targets after nonpredictive random sequences (random), random preceding standards (standards), and the three standards comprising the predicting sequence (n-3, n-2, and n-1, n-1 being the last most-informative stimulus). To have comparable ERPs in the predicted versus the random targets, only the random targets that were preceded by 3 to 10 random standards were included in the analysis. There were comparable number of trials for predicted (61 ± 5 auditory and 62 ± 8 visual) and random target (61 ± 6 auditory and 66 ± 8 visual) conditions after removal of misses and artifacts. We also evaluated P3 amplitude at Pz for each of the three standards presented randomly, that is, not as a part of the predictive sequence (Sn-1, Sn-2 and Sn-3) in order to compare each of these standards to its counterpart when presented within the predictive sequence.

For scalp distribution comparisons of P3b in the two target conditions, peak P3b amplitudes were measured in each condition across electrodes Fz, Cz, and Pz.

To demonstrate the early positive shift that was observed in the predicted target compared to the random target condition, a difference wave (DW) subtracting random targets from predicted targets was evaluated

at Fz, Cz, and Pz. Peak amplitude and latency were evaluated for this DW by determining the most positive point in the latency range of 150–350 msec in both modalities.

To compare the early perceptual processes between the two target conditions, peak N1 amplitudes (measured in microvolts) were determined at Fz for the auditory modality and at PO7 and PO8 in the visual modality for both predicted and random targets. We also assessed the contingent negative variation (CNV) to examine whether local context influenced preparatory attention during the detection of the predictive sequence (Walter, Cooper, Aldridge, McCallum, & Winter, 1964). CNV epochs were set from −200 to 1100 msec relative to stimulus onset. CNV was evaluated as the mean amplitude (measured in microvolts) for the range of 900–1100 msec poststimulus onset at midline electrodes (Fz, FCz, Cz, and CPz). CNV was evaluated for the three standards consisting of the predictive sequence (n-1, n-2, and n-3) and also for the random standard preceding the predictive sequence (n-4).

Analysis of variance (ANOVA) was performed with the Greenhouse–Geisser correction, followed by post hoc parametric paired t tests, Sidak corrected for multiple comparisons unless otherwise stated. Mean values with *SEM* are used throughout the text.

Single-trial Analysis

ERPs components such as the P3b are known to vary from trial to trial in both amplitude and latency (Holm et al., 2006; Truccolo, Ding, Knuth, Nakamura, & Bressler, 2002; Kutas et al., 1977). Thus, single-trial amplitude and latency may contribute additional information not contained in the ERP. We augmented the ERP analysis by further subjecting the P3b data to the analysis of a technique called ASEO, which stands for analysis of single-trial event-related potentials and ongoing activity (Xu et al., in press). In this method, the single-trial EEG is modeled as the linear combination of multiple event-related components that are relatively phase-locked to the onset of stimulus and ongoing activity (Chen, Bressler, Knuth, Truccolo, & Ding, 2006; Truccolo et al., 2002). In this Variable Signal Plus Ongoing Activity (VSPOA) model, the ongoing activity is considered an autoregressive (AR) random process. ASEO estimates the single-trial parameters, such as amplitudes and latencies of the ERP components, and the ongoing activity in two steps. In the frequency step, based on the most recently available estimate of the power spectrum of the ongoing activity, the waveforms of the ERP components and their single-trial parameters are estimated in the frequency domain by the maximum likelihood method. In the time step, the AR model parameters of the ongoing activity are estimated in the time domain based on the most recently estimated ERP parameters using an approximate maximum likelihood method. These two steps are iterated until no further improvement is seen in the estimated quantities.

EEG signals were filtered (0.5–50 Hz) and downsampled to 256 Hz. One component between 180 msec (auditory) or 200 msec (visual) and 800 msec poststimulus presentation was investigated at Pz for targets following both predictive and nonpredictive random sequences. Distributions were obtained for both peak P3b amplitude and latency. A Kolmogorov–Smirnov test showed these variables to be nonnormally distributed. Thus, the post hoc Mann–Whitney U test was used to compare the distributions between predictable and random nonpredictable conditions. Spearman's correlations were computed between peak P3b amplitude and latency across trials in each condition (predicted and random targets) for each subject (total of 24 correlations in each modality).

RESULTS

Behavioral Results

Mean accuracy was 94 ± 2% and 97 ± 1% for the auditory and visual tasks, respectively. Paired t tests showed that the reaction times (RT) for the predicted targets (mean RT = 325 ± 32 msec and 320 ± 25 msec for auditory and visual, respectively) were shorter than those for random targets (mean RT = 452 ± 12 msec and 476 ± 16 msec for auditory and visual, respectively) in both the auditory and visual modalities [$t(11) = 4.60$, $p = .001$ and $t(11) = 6.33$, $p < .0001$ for auditory and visual, respectively]. RT values are illustrated in Figure 2.

P3b

Grand-averaged ERPs across the 12 subjects at Pz elicited by random, predicted targets, standards, and the three standards constituting the predicting sequence (n-3, n-2, and n-1, n-1 being the last most-informative stimulus) are shown for the auditory modality in Figure 3A and for

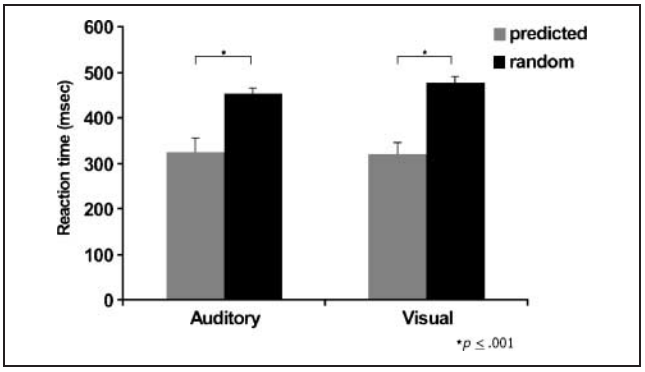

Figure 2. Reaction times for predicted and random targets in the auditory and visual modalities. Bars = standard errors of mean.

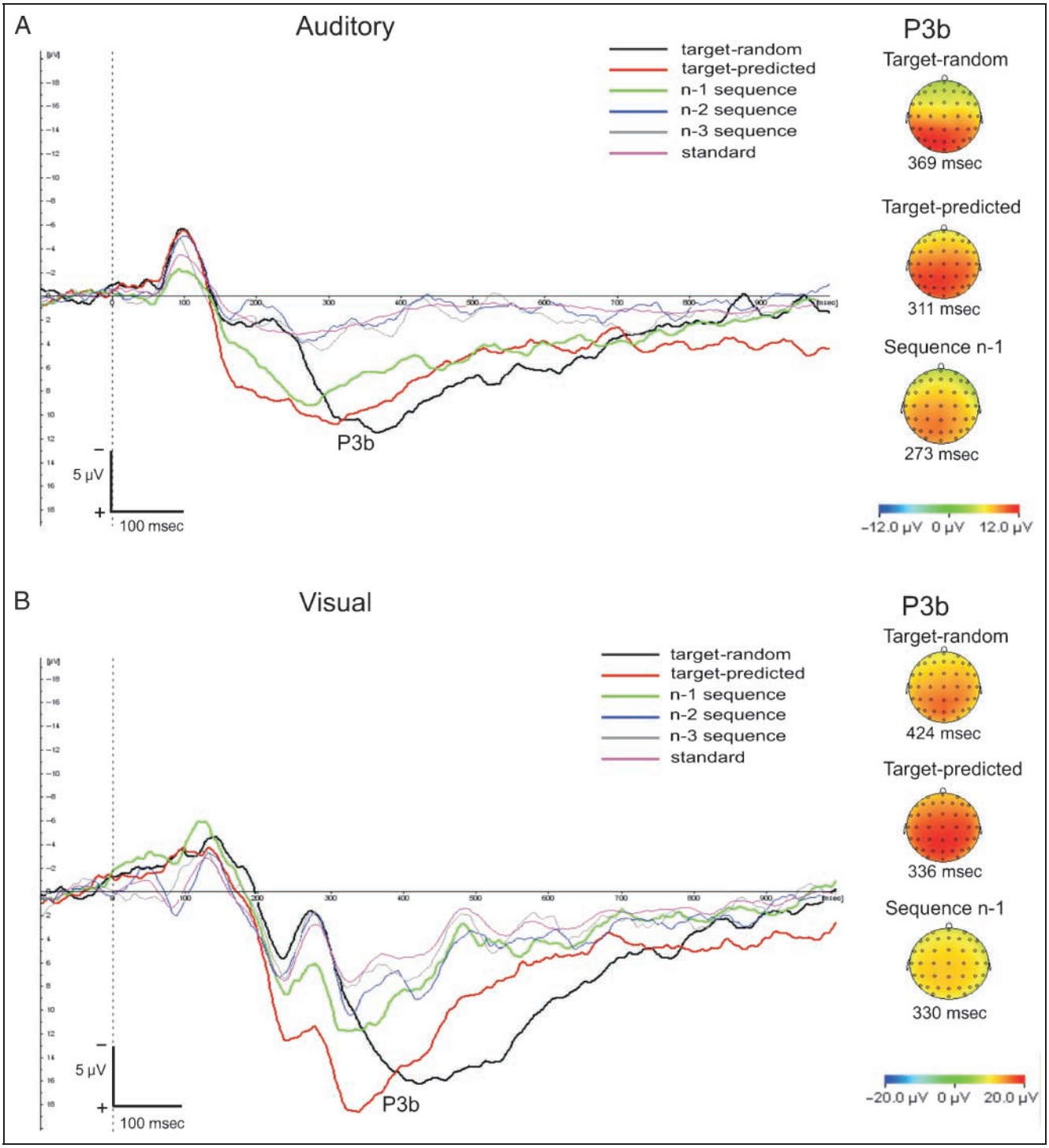

Figure 3. Grand average (n = 12) at Pz for the six conditions: targets after non predictive (random) and predictive sequences (predicted), the three standards comprising the predicting sequence (n-3, n-2, n-1), and random preceding standards (standards) for auditory (A) and visual (B) modalities. Topographical maps for the peak P3b are shown for random, predicted, and n-1 conditions.

the visual modality in Figure 3B. Both modalities show a robust posterior P3 component for targets with a shift in latency between predicted and random targets.

We performed four separate ANOVAs for each modality (auditory and visual) and for each peak P3b variable (amplitude and latency), with condition (random, predicted targets, standards, and the three standards comprising the predicting sequence: n-3, n-2, and n-1) as a factor.

There was a main effect for condition in the comparison of peak P3b latency in both the auditory [$F(5, 55) = 5.04$, $p = .003$] and visual [$F(5, 55) = 8.68$, $p < .0001$] modalities. Post hoc t tests showed that peak P3b latency was shorter for predicted targets (mean = 288 ± 14 msec

and 347 ± 11 msec for auditory and visual, respectively) compared to the peak P3b latency for random targets [mean = 375 ± 15 msec and 455 ± 20 msec for auditory and visual, respectively; $t(11) = 4.35$, $p = .001$ for auditory and $t(11) = 4.70$, $p = .001$ for visual]. These comparisons are displayed in Figure 4.

There was a main effect for condition in the comparison of peak P3b amplitude across the six conditions in the auditory [$F(5, 55) = 28.76$, $p < .0001$] and visual [$F(5, 55) = 14.39$, $p < .0001$] modalities. In the auditory modality, post hoc tests, corrected for multiple comparisons, showed that peak P3b amplitude was larger in predicted targets (13.19 ± 1.08 μV), random targets (13.63 ± 1.57 μV), and n-1 (10.32 ± 1.40 μV) compared to standards (4.14 ± 0.78 μV, $p < .01$), n-3 (6.09 ± 0.70 μV, $p < .05$) and n-2 (5.70 ± 0.95 μV, $p < .01$). However, there was no significant difference in P3b amplitude between random and predicted targets. Further analysis of each of the predictive standards n-1, n-2, and n-3 compared to each of these standards presented randomly (Sn-1, Sn-2, Sn-3) showed P3b amplitudes in n-1 (10.32 ± 1.40 μV) to be larger compared to Sn-1 [3.66 ± 0.67 μV, $t(11) = 6.93$, $p < .0001$], n-2 (5.70 ± 0.95 μV) was larger compared to Sn-2 [3.70 ± 0.99 μV, $t(11) = 2.77$, $p = .02$], and n-3 (6.09 ± 0.70 μV) was larger compared to Sn-3 [4.02 ± 0.67 μV, $t(11) = 3.35$, $p = .006$]. In the visual modality, post hoc tests corrected for multiple comparisons, showed peak P3b amplitude to be larger in predicted (20.55 ± 1.96 μV) and random (20.37 ± 1.91 μV) targets compared to standards (9.13 ± 0.88 μV, $p = .001$) and compared to n-3 (11.44 ± 1.35 μV, $p = .002$). However, there was no significant difference in P3b amplitude between random and predicted targets. Further analysis of each of the predictive standards n-1, n-2 and n-3 compared to each of these standards presented randomly (Sn-1, Sn-2, Sn-3) showed P3b amplitudes in n-1 (14.31 ± 1.85 μV) to be larger compared to Sn-1 [9.04 ± 0.92 μV, $t(11) = 3.22$, $p = .008$], there was a trend for n-2 (12.98 ± 2.10 μV) to be larger than Sn-2 [9.02 ± 0.87 μV, $t(11) = 2.16$, $p = .05$], and n-3 (11.44 ± 1.35 μV) was larger compared to Sn-3 [9.39 ± 0.86 μV, $t(11) = 2.73$, $p = .02$]. Figure 5 demonstrates the gradual increase in amplitude with increasing task relevance of the stimuli in both the auditory (Figure 5A) and visual (Figure 5B) modalities.

To compare scalp distributions of the target conditions, we performed an ANOVA with electrode (Fz, Cz, and Pz) and condition (predicted and random targets) as factors in each modality. There was a main effect for electrode in the auditory [$F(2, 22) = 45.71$, $p < .0001$] and visual [$F(2, 22) = 20.04$, $p < .0001$] modalities. There was no significant main effect for condition in both modalities. Post hoc assessment showed P3b amplitude at Pz to be larger than those at Cz for random targets [10.51 ± 1.93 μV, $t(11) = 4.07$, $p = .002$] and to be larger than Fz for both predicted [8.80 ± 1.61 μV, $t(11) = 4.75$, $p = .001$] and random [7.58 ± 1.72 μV, $t(11) = 6.96$, $p < .0001$] targets, in the auditory modality. P3b amplitudes were larger at Pz that at Fz for both predicted [15.72 ± 1.76 μV, $t(11) = 4.95$, $p < .0001$] and random [15.11 ± 1.87 μV, $t(11) = 3.63$, $p = .004$] targets in the visual modality. Scalp distributions of predicted and random targets are illustrated in Figure 6.

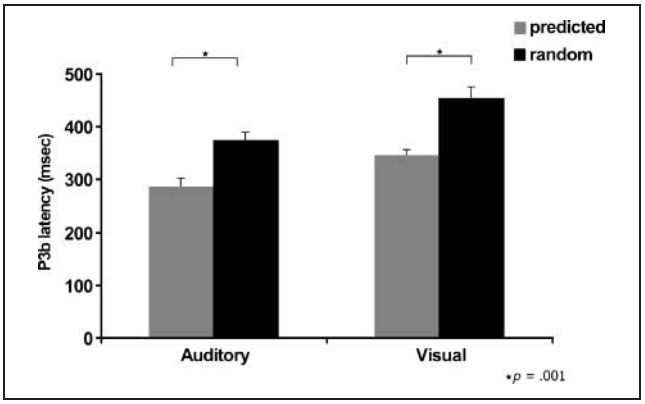

Figure 4. P3b peak latency at Pz for predicted and random targets in the auditory and visual modalities. Bars = standard errors of mean.

One-sample t test showed a significant DW at Pz (mean amplitude = 9.02 ± 1.17 μV, for auditory and 12.14 ± 1.87 μV, for visual) in both modalities [$t(11) = 7.66$, $p < .0001$ for auditory; $t(11) = 6.50$, $p < .0001$ for visual], demonstrating the early (mean latency = 236 ± 8 msec and 280 ± 7 msec for auditory and visual, respectively) positive shift observed in the predicted target compared to the random target condition. To compare the scalp distribution of the DW, an ANOVA with electrode (Fz, Cz, and Pz) as a factor was performed. There was a main effect for electrode in the auditory [$F(2, 22) = 4.36$, $p = .04$] and visual [$F(2, 22) = 25.38$, $p < .0001$] modalities. Post hoc assessment showed DW amplitude at Pz and Cz (8.52 ± 1.18 μV) to be larger than those at Fz [6.96 ± 0.79 μV, $t(11) = 2.22$, $p = .048$ and $t(11) = 2.83$, $p = .016$, respectively] in the auditory modality. DW amplitudes were larger at Pz than at Cz [10.80 ± 1.98 μV, $t(11) = 2.29$, $p = .04$] and Fz [7.73 ± 1.72 μV, $t(11) = 6.62$, $p < .0001$], and amplitude at Cz was larger than at Fz [$t(11) = 4.74$, $p = .001$] in the visual modality. Thus, this DW has a posterior-parietal scalp distribution similar to that of P3b in both modalities as is illustrated in Figure 6.

Pearson's correlations between auditory and visual P3b amplitudes across the 10 subjects that had recordings from both modalities showed that these covaried for both predicted ($r = .742$, $p = .01$) and random ($r = .645$, $p = .04$) targets.

N1

A paired t test comparing the peak N1 amplitude at Fz between predicted and random targets in the auditory modality showed no significant differences. We utilized

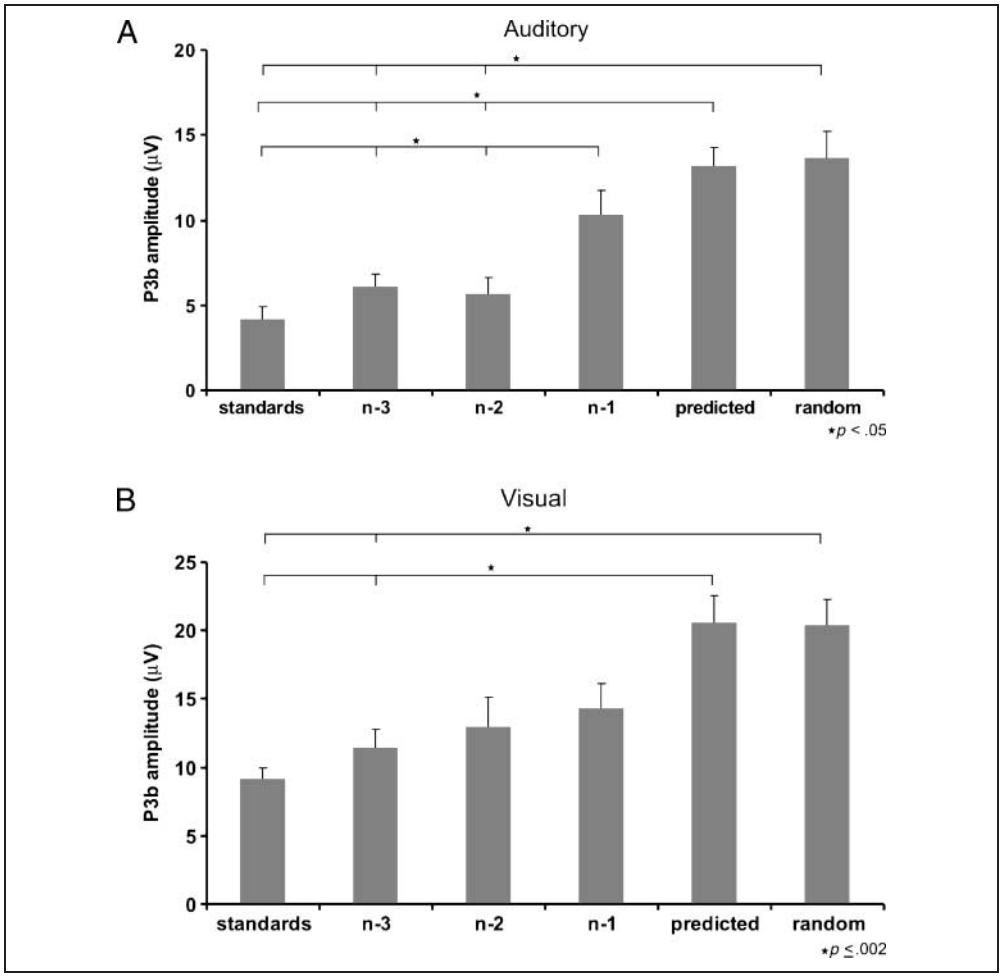

Figure 5. P3b peak amplitude for the six conditions: targets after nonpredictive (random) and predictive sequences (predicted), the three standards comprising the predicting sequence (n-3, n-2, n-1), and random preceding standards (standards) in the auditory (A) and visual (B) modalities. Bars = standard errors of mean.

an ANOVA with electrode (PO7 and PO8) and condition (predicted and random targets) as factors to compare the peak N1 amplitude between predicted and random targets in the visual modality. There was no significant main effect for condition or electrode. N1 ERPs are illustrated in Figure 7.

Contingent Negative Variation

For the comparison of the mean CNV amplitude, we collapsed the data from the standards consisting of the predictive sequence n-1 and n-2 and called this condition ''informative,'' and the data from the standard n-3 of the predictive sequence and the random standard before the sequence (n-4) and called this condition ''noninformative.'' We performed two separate ANOVAs for the auditory and visual modalities, with electrode (Fz, FCz, Cz, and CPz) and condition (informative, not informative) as factors. In the auditory modality, there was a significant main effect for condition [$F(1, 11) = 10.43$, $p = .008$], but no significant main effect for electrode. Post hoc t tests showed larger mean CNV amplitude in the informative compared to the noninformative condition at CPz [$t(11) = 3.81$, $p = .003$], Cz [$t(11) = 2.83$, $p = .02$], FCz [$t(11) = 2.72$, $p = .02$] and Fz [$t(11) = 2.53$, $p = .03$]. In the visual modality, there was no significant main effect for condition or electrode, although a similar effect was observed to that in the auditory modality. CNV results are illustrated in Figure 8.

ASEO Single-trial Analysis of Target P3b

Because P3b amplitude showed no significant difference between the two target conditions, we applied a novel single-trial method (ASEO) to further explore the reliability of this null effect for P3b amplitude. ASEO estimated single-trial amplitude and latency for a typical subject are shown in Figure 9A (auditory) and Figure 9B (visual). Although no difference is seen in the amplitude distributions, P3b latency is clearly shorter for the predicted than for the random condition. This is consistent with the ERP findings reported earlier. The results for all 12 subjects are illustrated in Figure 9C for the auditory modality and in Figure 9D for the visual modality, where each subject's P3b amplitude and latency were normalized using a Z-transformation so that the population results could be displayed. Significant decreases were found for single-trial P3b latencies ($p < .05$) in the

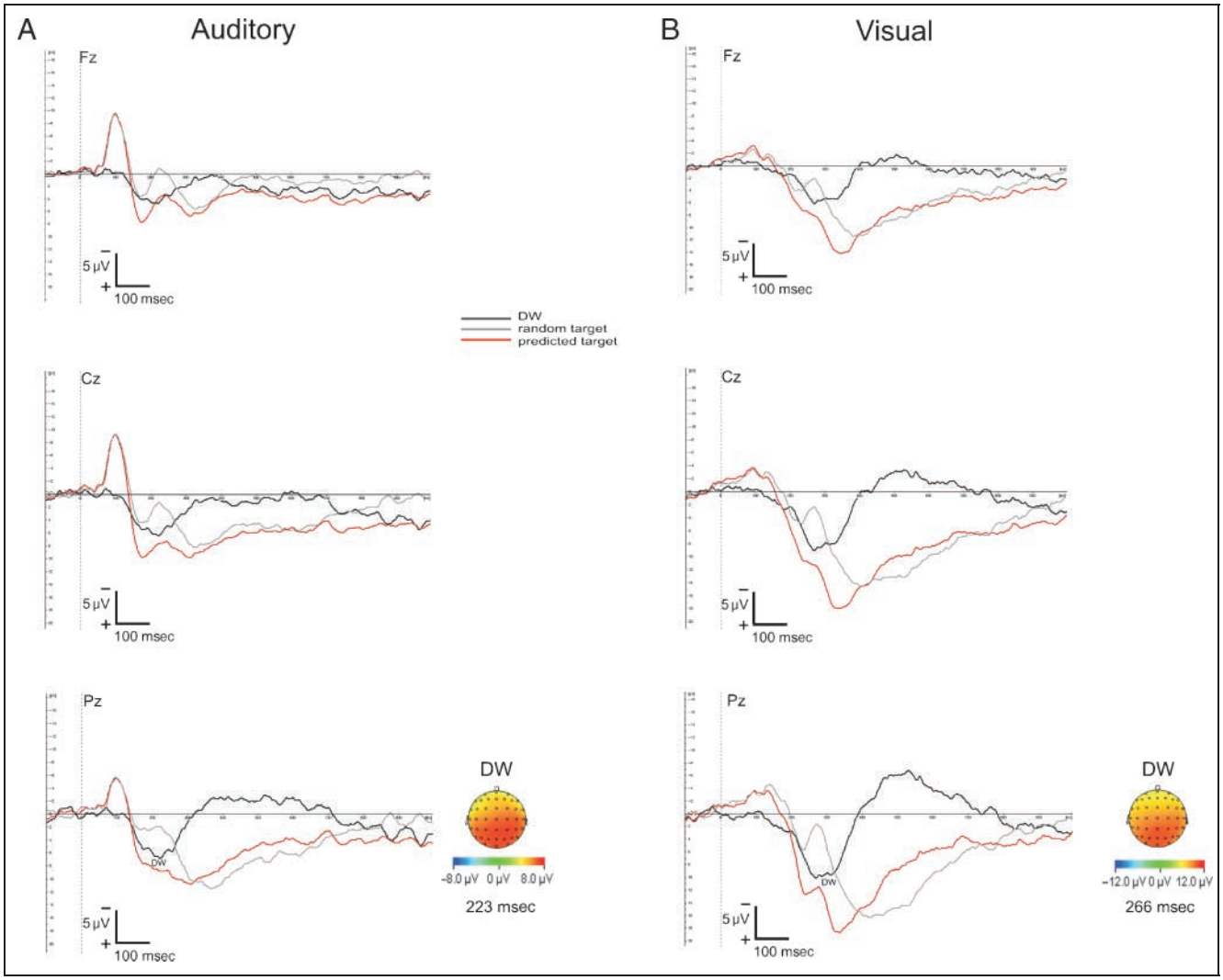

Figure 6. Grand average (n = 12) for the difference wave (DW) between predicted and random targets at electrode sites Fz, Cz, and Pz in the auditory (A) and visual (B) modalities. Topographical maps for the peak DW at Pz are displayed.

predictable compared with the random nonpredictable condition in 10/12 subjects (p = .003, Fisher's exact test) for the auditory modality and in 11/12 subjects (p = .001, Fisher's exact test) for the visual modality. Single-trial P3b amplitudes, however, showed no significant differences for the predictable compared with the random nonpredictable condition in 8/12 subjects in both modalities.

The relation between single-trial P3b amplitude and latency was addressed by a correlation analysis. We found no significant correlations between the two variables in 42/48 cases (20/24 for auditory, 22/24 for visual). The mean correlations between P3b amplitude and P3b latency in the auditory modality were −0.11 ± 0.1 for predicted targets and 0.10 ± 0.07 for random targets. The mean correlations between P3b amplitude and P3b latency in the visual modality were −0.06 ± 0.07 for predicted targets and 0.10 ± 0.09 for random targets. The independence of the two variables is also evident in the scatterplots in Figure 9A to D. ASEO reliably discriminated between predictable and random nonpredictable conditions (Figure 9) in both modalities, showing reduced P3b latencies of the predictable targets.

DISCUSSION

This study demonstrated that predictive local context affects target detection by reducing the duration of stimulus evaluation. This effect was associated with both faster RTs and shortened P3b latencies. P3b amplitude increased with task-informative stimuli, reaching its maximum in the two target conditions. However, there were no significant differences in P3b amplitude between predicted and random targets, suggesting that, in this easy discrimination task, local prediction only affected speed of processing. Importantly, these local context effects were independent of the sensory modality of the stimulus. A novel single-trial analysis provided further support for these findings. The P3b latency

estimated on a trial-by-trial basis reliably discriminated between predictable and random nonpredictable conditions and no significant correlations between P3b amplitude and latency were observed for either the predicted or the random targets, suggesting that these two variables were independently modulated.

P3b Latency and Duration of Stimulus Evaluation

P3b latency was shorter for sequence predicted targets than for targets after nonpredictive sequences. These results were confirmed by ASEO single-trial analysis, which discriminated reliably between predicted and random targets. In addition, we found that the P3 latency shift was related to an early positive shift, with a similar posterior-parietal scalp distribution as that observed for the P3b. This earlier positive shift was only seen in the predicted target as compared to the random target condition. This early positivity may reflect an early template match and suggests that P3b reflects processes of detection or preparatory attention of working memory rather than decision closure. The finding that P3b latency is shortened by task-informative preceding stimuli is supported by evidence from earlier studies (Duncan-Johnson & Donchin, 1982; Duncan-Johnson, 1981), showing that P3b latency is shorter for highly probable targets (80% predictable) than for less probable targets (20% predictable). P3b latency has been shown to be sensitive to the duration of the stimulus evaluation process (Hillyard & Kutas, 1983; Ford, Duncan-Johnson, Pfefferbaum, & Kopell, 1982; Duncan-Johnson, 1981; McCarthy & Donchin, 1981; Kutas et al., 1977). Furthermore, our findings suggest that this facilitation in stimulus evaluation is cognitive rather than perceptual, as targets were identical in their physical features and there were no significant N1 amplitude differences between predicted and random targets (Hillyard & Kutas, 1983). Latency differences in our study were associated with parallel behavioral results showing shorter RTs for predicted targets. This is in line with studies showing RTs to be correlated with P3b latencies in easy discrimination tasks requiring accuracy (Verleger, 1997; Kutas et al., 1977), such as the task utilized here.

P3b Amplitude and Task Relevance

The major findings regarding the effects of local context on P3b amplitude were twofold. First, we found that the

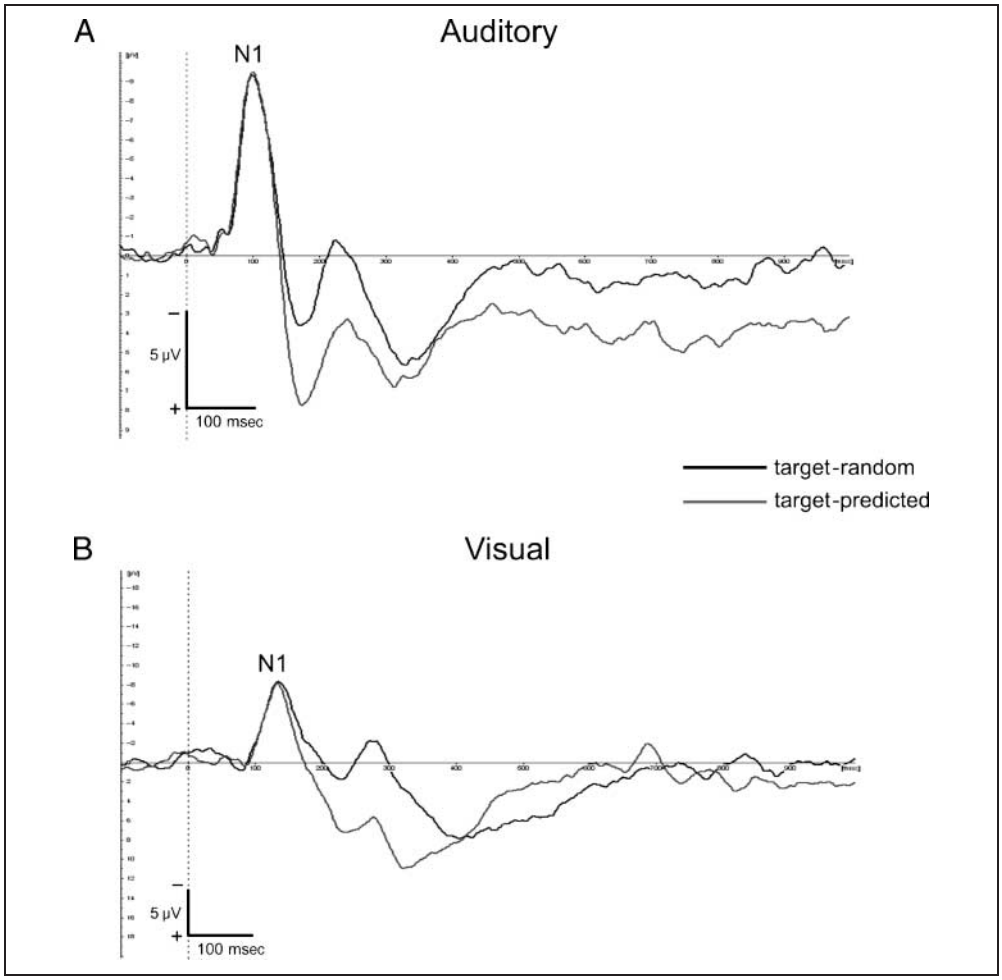

Figure 7. Grand average (n = 12) for predicted and random targets at Fz in the auditory modality (A) and at PO8 in the visual modality (B), illustrating that N1 is not different in the two target conditions.

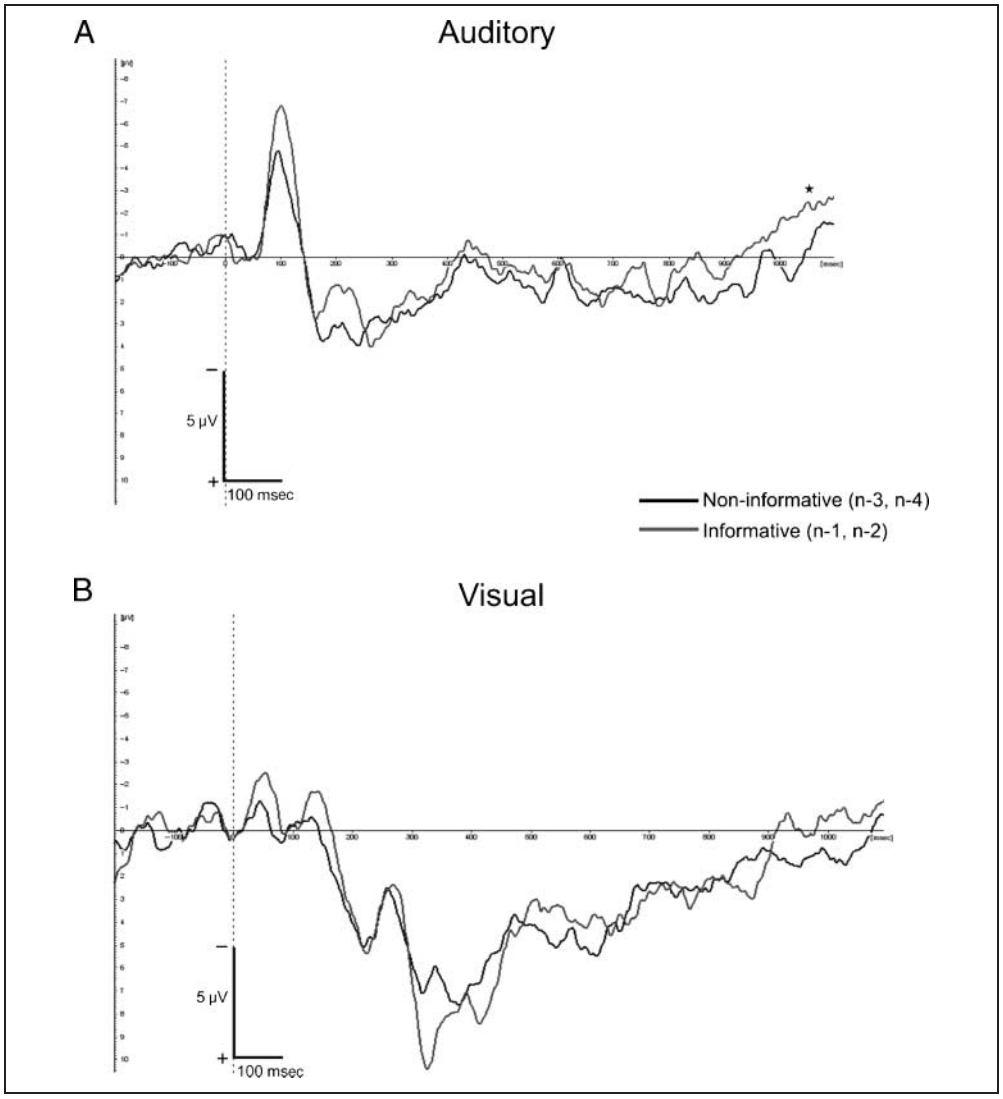

Figure 8. Grand average (n = 12) for standards containing predictive information (n-1 and n-2, informative condition) and for standards containing no predictive information (n-3, n-4, noninformative condition) regarding the subsequent target at CPz in the auditory modality (A) and at Cz in the visual modality (B). These electrodes showed the greatest change in mean CNV amplitude between 900 and 1100 msec poststimulus presentation, with significance difference ($p < .05$, indicated by the star) in the auditory modality.

P3b amplitude increased gradually with task relevance, with a significant P3b induced by the last most-informative standard of the predicting sequence, and the largest P3b for targets. This is supported by Sawaki and Katayama (2006), who have also shown that P3b amplitude increases as a function of task relevance. Because the predicting sequence induced a significant P3b compared to the same standards presented in a randomized nonpredictive sequence, it seems that it became a secondary target for the subjects. The increase in P3b amplitude in the predictive sequence supports an accumulation of information from the preceding trials. This is also supported by a significant increase in CNV in the auditory modality between stimuli with predictive context compared to those without predictive information. The increase in CNV indicates increased preparatory attention (Walter et al., 1964) to the more informative stimuli of the sequence.

Second, we demonstrated comparable P3b amplitudes for random and predicted targets with both conventional averaging and single-trial analysis. This is supported by Barcelo and Knight (2007), who showed no effect of contextual predictability on P3b amplitudes, and by Munson, Ruchkin, Ritter, Sutton, and Squires (1984), who showed in their study that there were no significant differences in P3b amplitude between correctly predicted and incorrectly predicted stimuli. However, our finding does contradict evidence showing that P3b amplitude decreases with the degree of expectancy (Donchin & Coles, 1988; Johnson, 1986; Squires et al., 1976; Sutton et al., 1967) or prediction (Suwazano, Machado, & Knight, 2000; Duncan-Johnson & Donchin, 1982). Numerous studies have demonstrated the effect of decision confidence on P3b amplitude (Parasurman, Richer, & Beatty, 1982; Squires et al., 1973, 1975; Hillyard, Squires, Bauer, & Lindsay, 1971). These studies document that the greater the decision confidence, the larger and earlier the P3b. We used a simple discrimination task, and it may be the case that the decision confidence was similar in the detection of a random target to that of a predicted target, and thus, no significant amplitude differences were observed. However, we cannot rule out

the possibility that a greater decision confidence in the detection of the predicted targets leads to earlier P3s. The fact that these results differ from those of earlier studies examining prediction effects (Suwazano et al., 2000; Duncan-Johnson & Donchin, 1982) may be due to differences in the design of the tasks. Duncan-Johnson and Donchin (1982) manipulated the probability (.20, .80, .50) of pairs of stimuli, where the second stimulus had to be predicted given the first stimulus. This task has a higher degree of difficulty than the prediction task used in the current study, and therefore, decision confidence may have been significantly affected. Suwazano et al. (2000), who examined the effects of the predictive value of novels on target detection, found P3b amplitude to be larger for nonpredictive (40% and 20%) compared to 100% predictive targets. It is difficult to compare these results with our study because shorter ISIs (200–900 msec) were used and the task was more difficult. In addition, novel stimuli employed in the Suwazano et al. study introduced either alerting or distracting elements according to the predictive information they contained, and thus, any amplitude changes observed may have arisen from the interaction between novelty and predictive effects.

In contrast, our study used the standards themselves, rather than introducing novel stimuli, in order to provide predictive information about the targets. Our use of three standards is an important difference in comparison to most of the studies performed to date, which have employed only one standard. The implication of this change is that sequential expectancies that are generated when a series of repeated standards are displayed may not apply here. Therefore, the large P3b that is generated when a sequence of standards is discontinued, as compared to an expected repeated continuation of standards (Donchin & Coles, 1988; Squires et al., 1976), may not be an appropriate comparison with our study of predicted expectations.

We propose that effects of expectancy of pattern continuation were abolished in our task and what determined the magnitude of the P3b amplitude was the task relevance of the stimulus. Hence, no P3b amplitude differences were observed between the predicted and random targets because those were both equally relevant for the performance of the task.

The advantage of the current paradigm was that it minimized the variables effecting P3b as much as possible,

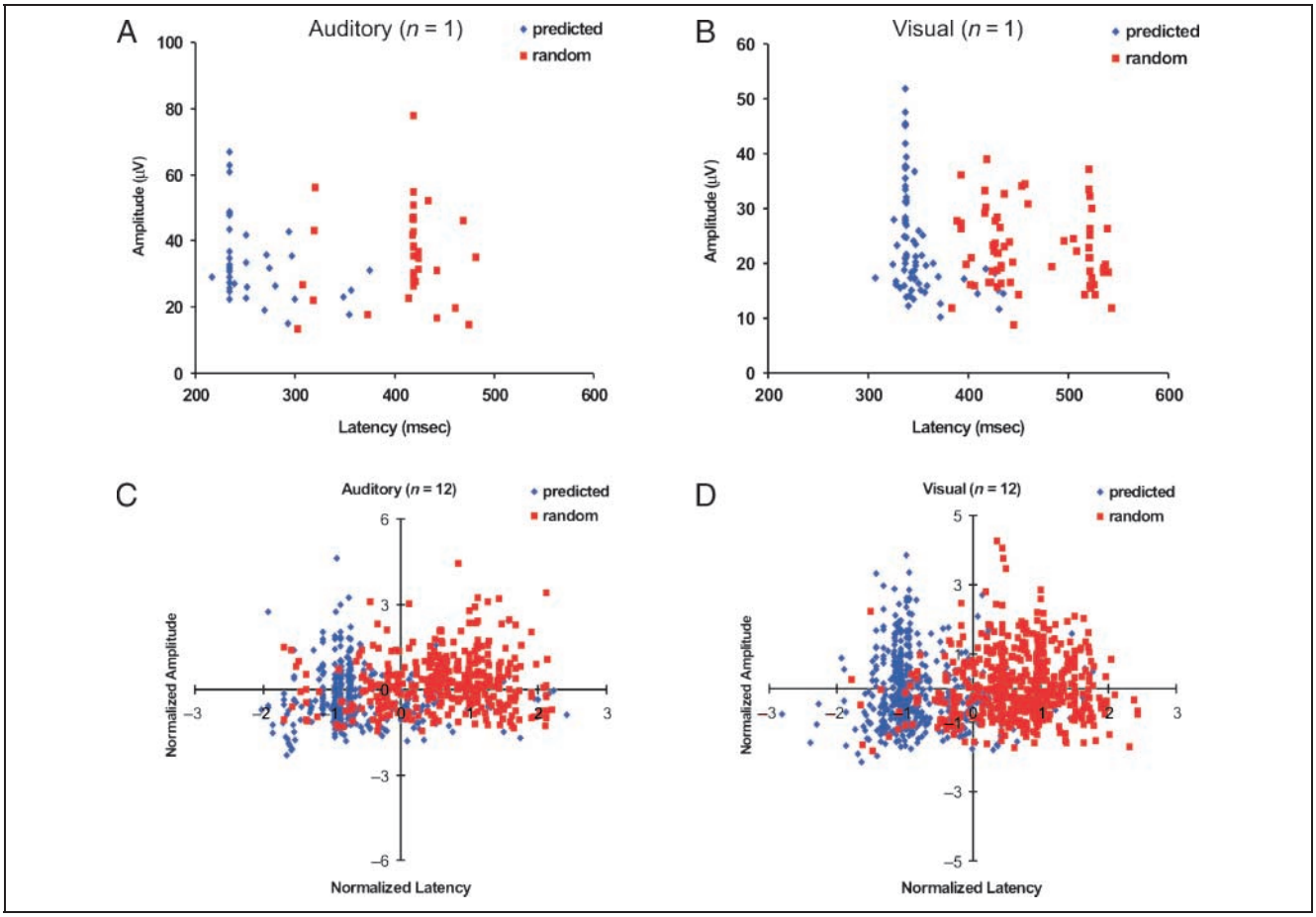

Figure 9. Single-trial P3b amplitude and latencies for predicted and random targets are plotted for auditory (A) and visual (B) modalities (n = 1). Normalized values (Z-transformed) of P3b amplitude and latency of predicted and random targets in all 12 subjects plotted for the auditory (C) and visual (D) modalities. Note that in all the plots latency is shorter, whereas amplitude is similar for predicted versus random targets.

such that discrimination difficulty was minimal, decision confidence of target detection was high, and predictive targets could be predicted with 100% certainty. In that light, it seems that in our study, predictive context only manipulated the duration of stimulus evaluation of predicted targets compared to random targets. Task relevance was manipulated with the build-up of contextual information (during the detection of the predictive sequence) and reached its maximum in both the predicted and random targets.

Modality-independent Effects of Local Context

Comparable effects of the predictive sequence on P3b amplitude and latency were demonstrated for both the auditory and visual sessions, suggesting a top–down modality-independent mechanism. This is in line with the hypothesis associating predictive context to prefrontal top–down control networks (Barcelo & Knight, 2007; Huettel et al., 2005; MacDonald et al., 2000, 2005; Barch et al., 2001; Miller & Cohen, 2001; Cohen & Servan-Schreiber, 1992). These studies provide evidence showing that the LPFC has a key role in the maintenance and representation of contextual information. Furthermore, the LPFC is also involved in top–down control of goal-oriented, context-appropriate responses and behavior (Barcelo & Knight, 2007; MacDonald et al., 2000, 2005; Cohen & Servan-Schreiber, 1992). This top–down control, also referred to as the ''internal representation of context'' (Cohen & Servan-Schreiber, 1992), involves updating and maintenance of task-relevant information in a form that can be used to select or execute appropriate responses. Contextual information may include a set of task instructions, specific prior stimuli, or the processing of a sequence of prior stimuli (Barch et al., 2001; Cohen & Servan-Schreiber, 1992). This is the type of information that subjects had to utilize in the present study, and therefore, it is reasonable to assume that the prefrontal cortex was engaged in the detection and prediction of targets during the task. Imaging studies have shown prefrontal activation, including the middle frontal gyrus, during target detection in a standard oddball task (Low, Leaver, Kramer, Fabiani, & Gratton, 2006; Kiehl, Laurens, Duty, Forster, & Liddle, 2001; McCarthy, Luby, Gore, & Goldman-Rakic, 1997). We propose that there is an additional contextual activation of the prefrontal cortex during the detection of predictive targets.

Independent Modulation of P3b Variables

Single-trial analysis allowed for correlations between latency and amplitude of the P3b component and showed that these two variables were not significantly correlated, and thus, may be modulated independently of each other. This is supported by pharmacological studies by Fowler and Mitchell (1997) and Fowler, Kelso, Landlot, and Porlier (1988), demonstrating differential effects of nitric oxide or barbiturate on P300 latency and amplitude, where only the P300 latency was affected (increased) by the drugs, and not P300 amplitude. In both of these studies, either no correlations (Fowler et al., 1988) or a low average positive correlation of .22 (Fowler & Mitchell, 1997) were found between P300 latency and P300 amplitude on a single trial basis, which is consistent with our results. The authors proposed the existence of independent mechanisms for the two variables affecting the P300 component, which is further supported by the findings of the present investigation, where local context had differential effects on P3b amplitude and latency.

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