Implicit anticipation of probabilistic regularities:

Larger CNV emerges for unpredictable events

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Abstract

Anticipation of upcoming events plays a crucial role in automatic behaviors. It is, however, still unclear whether the event-related brain potential (ERP) markers of anticipation could track the implicit acquisition of probabilistic regularities that can be considered as building blocks of automatic behaviors. Therefore, in a four-choice reaction time (RT) task performed by young adults (N = 36), the contingent negative variation (CNV) as an ERP marker of anticipation was measured from the onset of an uninformative warning signal until the presentation of the target stimulus. Due to the probability structure of the task, target stimuli were either predictable or unpredictable, but this was unknown to participants. Results showed that the CNV amplitude during response preparation was larger before the unpredictable than before the predictable stimuli. In addition, although RTs increased, the P3 amplitude decreased for the unpredictable as compared with the predictable stimuli, possibly due to the stronger response preparation that preceded stimulus presentation. These results suggest that enhanced attentional resources are allocated to the implicit anticipation and processing of unpredictable events. This possibly results from the formation of internal models on the probabilistic regularities of the stimulus stream, favoring predictable events. Overall, we provide ERP evidence for the implicit anticipation of probabilistic regularities, confirming the role of predictive processes in learning and memory.

Keywords: anticipation, contingent negative variation, internal models, implicit statistical learning, predictive processes, transitional probabilities

Introduction

Predicting future events is a core aspect of adaptive behavior. Predictions are guided by prior probabilities according to many theories of cognition, learning, and decision making (Daw, Gershman, Seymour, Dayan, & Dolan, 2011; Friston, 2005, 2010; Friston, Stephan, Montague, & Dolan, 2014; Gómez & Flores, 2011; Griffiths, Kemp, & Tenenbaum, 2008; Shohamy & Daw, 2015). Based on prior probabilities, the set of processes that facilitate perceptual, cognitive, and motor operations before their actual occurrence can be captured by the notion of anticipation (Hommel, 2009; van Boxtel & Böcker, 2004). Anticipation largely depends on the extraction and processing of probabilistic regularities organizing environmental events (e.g., Koelsch, Busch, Jentschke, & Rohrmeier, 2016; Maheu, Dehaene, & Meyniel, 2019; Meyniel, Maheu, & Dehaene, 2016), which have been found to be crucial in many automatized cognitive abilities (Armstrong, Frost, & Christiansen, 2017; Aslin, 2017; Conway, 2020). The presence and operation of anticipatory processes can be evidenced by reaction time (RT) changes and various measures derived from eye-tracking, electromyography, neuroimaging, and electrophysiology (e.g., Fan et al., 2007; Gómez & Flores, 2011; Killikelly & Szűcs, 2013; Medimorec, Milin, & Divjak, 2019; Tremblay & Saint-Aubin, 2009). Meanwhile, the question remains to what extent the electrophysiological markers of anticipation are sensitive to the processing of probabilistic regularities (Daltrozzo & Conway, 2014). Therefore, we investigate anticipatory processes by means of event-related brain potentials (ERPs) in an experimental setting that involves the implicit acquisition of predictable and unpredictable regularities underlying the ongoing sensorimotor stream.

A possible candidate among the slow cortical potentials related to anticipatory processes is the contingent negative variation (CNV). The CNV has usually been recorded in cued/forewarned RT tasks as an increasingly negative potential shift occurring over the frontal and central electrode sites in the time interval between a cue/warning/S1 stimulus and

a target/imperative/S2 stimulus requiring a response (Berchicci, Spinelli, & Di Russo, 2016; Brunia, 2003; Killikelly & Szűcs, 2013; Kononowicz & Penney, 2016; Leuthold, Sommer, & Ulrich, 2004; Molnár et al., 2008; Verleger, Paulick, Möcks, Smith, & Keller, 2013; Walter, Cooper, Aldridge, McCallum, & Winter, 1964). The CNV could be decomposed into multiple potentials: While the early phase of the component has been thought to reflect the orientation to the cue stimulus, the late phase could reflect the anticipatory activity for the target and the motor preparation of the related response (Loveless & Sanford, 1974; van Boxtel & Böcker, 2004; Weerts & Lang, 1973). The present study focuses on the late CNV, considering the uninformative nature of the cue stimulus and the relatively short cue-target interval (see section Stimuli, task, and procedure) that might not ensure the full development of the different composing waves (Berchicci et al., 2016; Di Russo et al., 2017).

Given the different composing waves and the various paradigms applied, the suggested functional role of the CNV and its interpretation are also numerous. Beyond the above-listed processes and the original suggestion that the CNV indicates stimulus expectancy (Walter et al., 1964), this component has been linked to, for instance, time processing (Macar & Vidal, 2004), proactive control (Killikelly & Szűcs, 2013), motor pre/re-programming (Anatürk & Jentzsch, 2015; Jentzsch, Leuthold, & Richard ridderinkhof, 2004; Leuthold & Jentzsch, 2002), the complexity of preparation (Cui et al., 2000; De Kleine & Van der Lubbe, 2011), feedback/reward anticipation (Hackley, Valle-Inclán, Masaki, & Hebert, 2014), and the amount of attentional resources or effort recruited and available for stimulus processing and response preparation (Cui et al., 2000; Emerson, Daltrozzo, & Conway, 2014; Pauletti et al., 2014; Stadler, Klimesch, Pouthas, & Ragot, 2006). Overall, the CNV is likely a marker of a task-specific preparatory state that tunes and optimizes perceptual, cognitive, and motor processes, supported by the activation of multiple sensory-motor brain areas and controlled by

the frontoparietal networks (Gómez & Flores, 2011; Kononowicz & Penney, 2016; Pauletti et al., 2014).

So far, only a few studies have examined directly the sensitivity of the CNV to the probabilistic regularities underlying a stimulus sequence while implicitly acquiring the sequence per se (Daltrozzo & Conway, 2014). In a visual S1-S2 associative learning task, the CNV amplitude decreased before the S2 in the predictable condition while it increased in the unpredictable condition as the acquisition of the probability structure progressed (Rose, Verleger, & Wascher, 2001). Meanwhile, the CNV amplitude increased for regular vs. random targets in an auditory learning-oddball task (Jongsma et al., 2006) and for possible vs. impossible target occurrence in another oddball task with tone pairs (Stadler et al., 2006). A further auditory sequential learning task showed that the CNV emerged only after the high- and low-probability predictor tones and not after the zero-probability predictors (Emerson et al., 2014). Overall, it seems that either enhanced or decreased CNV amplitudes could indicate the sensitivity to probabilistic regularities.

In this study, therefore, we aim to measure implicit anticipatory processes in a four-choice RT task that, unknown to participants, includes a sequential regularity between non-adjacent trials yielding a probability structure with predictable and unpredictable stimuli. By means of RTs, using a version of this task, we have already shown that the implicitly acquired prior knowledge on the probabilistic regularities influenced the processing of further stimuli lacking a predictable structure (Kóbor, Horváth, Kardos, Nemeth, & Janacsek, 2019). We assumed that this persistence of knowledge occurred through the formation of internal models. Therefore, it is conceivable that anticipatory processes based on similar internal models would start to operate before each stimulus is presented, at least after the probability structure of the task has been acquired. Because of these internal models, the anticipation of predictable stimuli and the preparation of appropriate responses possibly become automatic

and require less attentional resources, as opposed to the unpredictable stimuli (Horváth et al., under review). Accordingly, considering the functional significance of the CNV, its amplitude is expected to be larger for unpredictable than for predictable stimuli. In parallel, according to other behavioral studies with this task (e.g., D. V. Howard et al., 2004; Nemeth et al., 2010; Takács et al., 2018; Tóth et al., 2017), we expect slower RTs to unpredictable than to predictable stimuli.

Method

Participants

Thirty-six healthy young adults (23 females) between the ages of 18 and 28 (*M* = 21.6, *SD* = 2.2) participated in the study. They were undergraduate students from Budapest, Hungary (years of education: *M* = 14.6, *SD* = 1.5). Handedness was assessed with the Edinburgh Handedness Inventory revised version (Dragovic, 2004a, 2004b; Oldfield, 1971), according to which the mean Laterality Quotient was 80.3 (*SD* = 35.3; -100 means complete left-handedness, 100 means complete right-handedness). Participants had normal or corrected-to-normal vision, and according to the pre-defined inclusion criteria, none of them reported a history of any neurological and/or psychiatric condition, and none of them was taking any psychoactive medication. They performed in the normal range on standard neuropsychological tests (Wisconsin Card Sorting Task [perseverative error percentage]: *M* = 10.42, *SD* = 2.23; Digit span task [mean short-term memory span; possible range: 3–9]: *M* = 6.31, *SD* = 1.31; Counting span task [mean working memory span; possible range: 2–6]: *M* = 3.64, *SD* = 0.72; Go/No-Go task [discriminability index: hit rate minus false alarm rate]: *M* = .76, *SD* = .15). All participants provided written informed consent before enrollment and received course credit for taking part in the experiment. The study was approved by the

United Ethical Review Committee for Research in Psychology (EPKEB) in Hungary and was conducted in accordance with the Declaration of Helsinki.

Stimuli, task, and procedure

Implicit acquisition of probabilistic regularities was measured by a modified cued version of the Alternating Serial Reaction Time (ASRT) task (Horváth et al., under review; Kóbor, Horváth, Kardos, Takács, et al., 2019; Kóbor et al., 2018; Nemeth et al., 2010). In this task version, an experimental trial consisted of the presentation of two subsequent stimuli: a cue and a target. First, a central fixation cross that served as the neutral, uninformative cue was presented for a fixed duration of 900 ms. Second, after this duration, the cue was replaced by an arrow stimulus that served as the target, presented at the center of the screen for a fixed duration of 200 ms (cf. Kóbor, Horváth, Kardos, Takács, et al., 2019; Kóbor et al., 2018). After target offset, a blank response window was displayed for a fixed duration of 700 ms. Then, the next trial started, yielding an 1800-ms-long inter-trial-interval that consisted of an anticipatory/response preparation phase (from cue onset to target onset) and a response execution phase (from target onset to the next cue onset, see Fig. 1A).

Participants were instructed to respond as quickly and accurately as possible to the direction of the target by pressing one of the four response keys of a Cedrus RB-530 response pad (Cedrus Corporation, San Pedro, CA). The spatial directions of the arrow stimuli were mapped onto the four response keys (left direction/left response key = left thumb, up = left index finger, down = right thumb, and right = right index finger). Participants were also asked to pay attention to and maintain their gaze on the fixation cross and try not to blink, because it was shortly followed by the target. If an incorrect response occurred, the fixation cross starting the next trial was presented in red color instead of the original black one. If no response occurred during target presentation or in the predefined response window (i.e.,

missing response), the fixation cross starting the next trial was presented in blue instead of black. Participants were informed that the color of the fixation cross would change if they did not provide the correct response. As the fixation cross did not convey information on the *following* target and only served as a warning signal, no other details were provided about its function. After an incorrect or missing response, although participants could provide further behavioral responses, this did not influence the presentation and timing of the next trial.

Unbeknownst to the participants, the arrow stimuli are presented according to an eight-element sequence, within which predetermined/pattern (P) and random (r) elements alternate with one another (see Fig. 1A). For instance, 2 – r – 1 – r – 3 – r – 4 – r is one of the sequences, where numbers denote the four predetermined spatial directions [1 = left, 2 = up, 3 = down, 4 = right] of the arrows and *r*s denote the randomly chosen directions out of the four possible ones (see Fig. 1B). There are 24 permutations of the four spatial directions that could determine the applied sequence; however, because of the continuous presentation of the stimuli, there are only six *unique* permutations: 1 – r – 2 – r – 3 – r – 4 – r, 1 – r – 2 – r – 4 – r – 3 – r, 1 – r – 3 – r – 2 – r – 4 – r, 1 – r – 3 – r – 4 – r – 2 – r, 1 – r – 4 – r – 2 – r – 3 – r, and 1 – r – 4 – r – 3 – r – 2 – r. Note that each of these six permutations can start at any position; e.g., 1 – r – 3 – r – 4 – r – 2 – r and 2 – r – 1 – r – 3 – r – 4 – r are identical sequence permutations. In this study, one of these six unique permutations was selected for each participant in a pseudorandom manner (see also J. H. Howard, Jr. & Howard, 1997; Kóbor, Horváth, Kardos, Takács, et al., 2019; Kóbor et al., 2018; Nemeth et al., 2010).

The alternating sequence yields a probability structure in which some chunks of three successive trials – hereafter referred to as *triplets* – are more probable than others. Thus, the construction of triplets could be considered as a method for identifying a hidden probability structure in the ASRT task. Particularly, while the third trials of some triplets are *probable* (predictable) continuations for the first trials, the third trials of other triplets are *less probable*

continuations for the first trials. The former triplets are referred to as *high-probability* triplets while the latter ones are referred to as *low-probability* triplets (e.g., Nemeth & Janacsek, 2011; Nemeth, Janacsek, Polner, & Kovacs, 2013). Accordingly, triplets are created throughout the entire stimulus set: Each trial (stimulus) is categorized as either the third trial of a high- or a low-probability triplet and the third trial of a triplet is also the second trial of the following triplet (Kóbor, Janacsek, Takács, & Nemeth, 2017; Kóbor et al., 2018; Szegedi-Hallgató et al., 2017). Consequently, please, note that the terms “trial” and “triplet” are used interchangeably for the remainder of the paper.

Because of the alternating sequence, although high-probability triplets could have P – r – P or r – P – r structure, low-probability triplets could only have a r – P – r structure (see Fig. 1B). In the case of the 2 – r – 1 – r – 3 – r – 4 – r sequence, 2 – X – 1, 1 – X – 3, 3 – X – 4, and 4 – X – 2 are high-probability triplets (X denotes the middle trial of the triplet), and, for instance, 1 – X – 2 and 4 – X – 3 are low-probability ones. From another perspective, random trials that are the 50% of all trials appear either with high or low probability, while pattern trials that are the other 50% of all trials always appear with high probability. Overall, the combination of the sequential and probability properties yields three possible trial types: pattern high-probability, random high-probability, and random low-probability triplets (occurring with an overall probability of 50%, 12.5%, and 37.5%, respectively; see Fig. 1B).

Random high-probability triplets could be considered as “accidentally-regular” random triplets, which are predictable but rarely occurring at the level of unique trials. These trials integrate characteristics related to both the alternating P – r – P – r sequence and the hidden probability structure (Kóbor, Horváth, Kardos, Takács, et al., 2019). In addition, some pre-existing response biases originating from higher levels of the alternating sequence have also been observed for these trials (Szegedi-Hallgató, Janacsek, & Nemeth, 2019). Therefore, to focus on contrasting the predictable pattern trials with the unpredictable random trials (i.e.,

pattern high-probability triplets vs. random low-probability triplets), all random high-probability triplets were excluded from the analyses (cf. Horváth et al., under review).

One block of the ASRT task contained 85 trials. In each block, the eight-element sequence repeated 10 times after five warm-up trials consisting only of random stimuli. After each block, participants received feedback (lasting for 4000 ms) about their mean reaction time and accuracy in the given block, then, they could have a short rest before starting the next block. Altogether 30 blocks were completed (2550 trials in total). The experimental procedure lasted about 2.5 hours, including the application and removal of the electrode cap. The ASRT task was written in and controlled by the Presentation software (v. 18.1, Neurobehavioral Systems). Stimuli were displayed on a 21” LCD screen at a viewing distance of 125 cm. Neuropsychological tests (see section Participants) were administered a few days before the EEG experiment during a one-hour-long session.

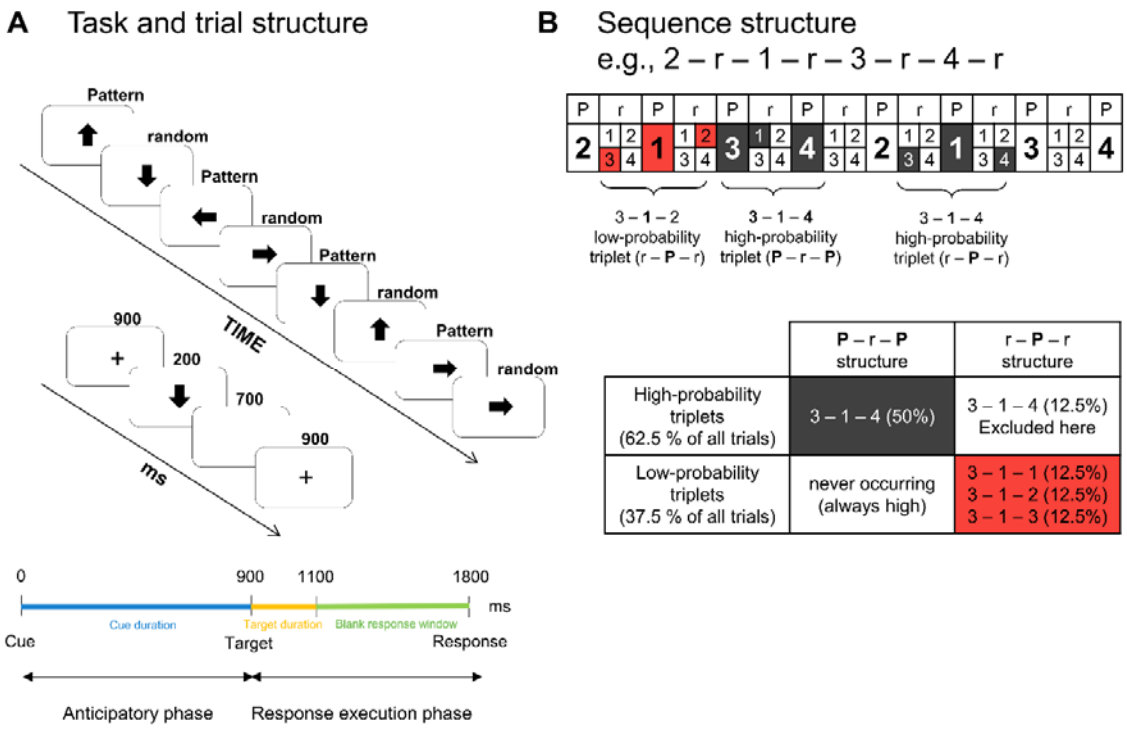

Figure 1. Design of the experiment. (A) In this version of the Alternating Serial Reaction Time (ASRT) task, a central fixation cross that serves as the neutral, uninformative cue is followed by an arrow stimulus that serves as the target. The duration of the cue is 900 ms, the duration of the target is 200 ms, and responses are recorded from target onset until the end of the trial (for altogether 900 ms). This yields a fixed 1800-ms-long inter-trial-interval. The presentation of the target stimuli follows an eight-element sequence, within which pattern (P) and random (r) elements alternate with one another. (B) In the alternating sequence structure, numbers denote the four spatial directions (1 = left, 2 = up, 3 = down, 4 = right) of the arrows. The alternating sequence makes some runs of three consecutive trials (triplets) more probable than others. High-probability triplets are denoted with dark-grey shading and low-probability triplets are denoted with coral shading. Each pattern and random trials are categorized as the last trial of a high- or a low-probability triplet, thus, three different trials occur: pattern high-probability (P – r – P structure), random high-probability (r – P – r structure), and random low-probability (r – P – r structure) trials. This study analyses only pattern high-probability or predictable (dark-grey shading in the lower table) and random low-probability or unpredictable trials (coral shading in the lower table).

EEG recording and analysis

The continuous EEG activity was recorded in an electrically shielded, acoustically attenuated, and dimly lit room using the actiCAP active electrode system with BrainAmp Standard

amplifier and BrainVision Recorder 1.2 software (BrainProducts GmbH, Gilching, Germany). The 64 sensors consisting of Ag/AgCl electrodes integrated with active circuits were mounted in an elastic cap and placed according to the 10% equidistant system. The FCz electrode was used as reference and the Fpz electrode was used as ground. The sampling rate was 1000 Hz. During recording, the impedance of the electrodes was kept below 10 kΩ.

The continuous EEG data were analyzed offline using the BrainVision Analyzer 2.1.2 software (BrainProducts GmbH). The pre-processing steps described below followed those presented in the Kóbor et al. (2018) and Kóbor, Horváth, Kardos, Takács, et al. (2019) papers with minor modifications (e.g., filter settings, length of the segment, number of time bins) to fit the purposes of the present study. First, after visual screening for major deflections, if necessary, bad electrodes were replaced by spline interpolation: A maximum of one electrode per participant (M = 0.14, SD = 0.35) was interpolated. Second, the EEG data were band-pass filtered within 0.03-30 Hz (48 dB/oct) and notch filtered at 50 Hz to remove additional electrical noise. Third, horizontal and vertical eye-movement artifacts and heartbeats were corrected with independent component analysis (Delorme, Sejnowski, & Makeig, 2007): Components between one and three per participant (M = 1.97, SD = 0.51) were rejected, then, the channel-based EEG data were recomposed. Fourth, EEG data were re-referenced to the average activity of all electrodes. Fifth, the continuous EEG data were segmented in two steps as follows. To track the temporal trajectory of acquisition, the data were cut into three, equally long time bins (periods), each containing ten consecutive blocks of the ASRT task. Next, within each period, segments were extracted from -200 to 1500 ms relative to cue onset, separately for pattern high-probability and random low-probability triplets. Only those correctly responded trials were included in this step of the segmentation that also followed correctly responded trials. Trials with any responses occurring during the response preparation phase (i.e., before the presentation of the target) were omitted from the analyses.

Altogether six (two triplet types * three periods) segment types were created for the cue-locked averages. Note that following the standard data analysis protocol established in previous studies using the ASRT task (e.g., J. H. Howard, Jr. & Howard, 1997; Kóbor et al., 2017; Nemeth, Janacsek, Polner, et al., 2013; Song, Howard, & Howard, 2007; Virag et al., 2015), two types of low-probability triplets – repetitions (e.g., 1 – 1 – 1, 4 – 4 – 4) and trills (e.g., 1 – 2 – 1, 2 – 4 – 2) – were eliminated from the ERP and the behavioral analyses, because pre-existing response tendencies have often been shown to them (D. V. Howard et al., 2004). Therefore, the low-probability triplet category consisted of low-probability triplets without trills and repetitions (but see Szegedi-Hallgató et al., 2019).

Following segmentation, to remove artifacts still present in the data after ICA corrections, an automatic artifact rejection algorithm implemented in the BrainVision Analyzer software was applied, which rejected segments where the activity exceeded +/- 100 µV at any of the electrode sites. The mean numbers of retained (artifact-free) segments were 331.9 (*SD* = 44.0, range: 186 – 379) for pattern high-probability triplets and 165.6 (*SD* = 24.4, range: 93 – 209) for random low-probability triplets. The retained segments were baseline corrected based on the mean activity from -200 ms to 0 ms (pre-cue baseline). Finally, these segments were averaged for the two triplet types in each of the three periods.

Grand average ERP waveforms calculated separately for each triplet type in each period as well as averaged for the entire acquisition phase across all periods were visually inspected to determine the latency range where the CNV component would emerge and vary as a function of triplet types. For both triplet types, at electrodes FCz and Cz, the CNV started to steeply increase around 700 ms after cue onset and showed maximal negativity at target onset. Since the late phase of this negativity, close to target onset, is assumed to reflect anticipatory and preparation process (see Introduction), the CNV was quantified as the mean amplitude between 800 ms and 900 ms after cue onset (cf. Boehm, van Maanen, Forstmann,

& van Rijn, 2014). Meanwhile, the difference waveforms calculated as ERPs for random low-probability triplets minus ERPs for pattern high-probability triplets were maximal over the central and centroparietal electrode sites (cf. Brunia & Damen, 1988; De Kleine & Van der Lubbe, 2011; Gómez, Marco, & Grau, 2003; Leynes, Allen, & Marsh, 1998; Verleger, Wauschkuhn, van der Lubbe, Jaśkowski, & Trillenberg, 2000). Therefore, based on the observed topographical distribution of the CNV difference waveform, a centroparietal (CP) electrode pool was defined by calculating the average activity of the electrodes C1, Cz, C2, CP1, CPz, CP2, P1, Pz, and P2. The CNV for all triplet types and periods was quantified over this centroparietal electrode pool.

The distribution of the between-triplets difference remained stable after target onset, which is in line with the observation that the CNV and the P3 components could overlap (Verleger, Paehge, Kolev, Yordanova, & Jaśkowski, 2006; Verleger et al., 2013; Verleger, Siller, Ouyang, & Śmigasiewicz, 2017). Therefore, the peak of the P3 and the late descending flank of the P3 (hereafter referred to as the late P3) were also examined over the same centroparietal electrode pool. The peak of the P3 was quantified as the mean amplitude between 1200 ms and 1300 ms after cue onset. The late P3 was quantified in the remaining interval of the segment, as the mean amplitude between 1300 ms and 1500 ms (cf. Kóbor, Horváth, Kardos, Takács, et al., 2019).

Data analysis

As in the case of the EEG data, ten-block-long segments of the behavioral data were grouped into three periods, labeled consecutively in this paper (1, 2, etc.). For each participant and period, separately for pattern high-probability and random low-probability triplets, median RT was calculated for those correct responses that also followed correct responses. Independent of triplet types, general skill improvements (faster RTs) reflecting more efficient visuomotor

and motor-motor coordination due to practice were also considered (cf. Hallgató, Győri-Dani, Pekár, Janacsek, & Nemeth, 2013; Juhasz, Nemeth, & Janacsek, 2019).

The mean accuracy of responding for each triplet type and period are provided in Table 1; otherwise, the paper focuses on the RT analysis (cf. Kóbor, Horváth, Kardos, Takács, et al., 2019; Kóbor et al., 2018). We have three reasons to do so: accuracy is influenced by (1) the feedback given to participants after each block; (2) the presentation of the cue increased the length of the trial that possibly provided more time for accurate response selection; and (3) overall accuracy has usually been high with relatively low variability in samples of healthy young adults performing the ASRT task (J. H. Howard, Jr. & Howard, 1997; Janacsek, Ambrus, Paulus, Antal, & Nemeth, 2015; Nemeth et al., 2010; Romano, Howard, & Howard, 2010).

The implicit acquisition and prediction of probabilistic regularities was quantified with two-way repeated measures analyses of variance (ANOVA) with Type (pattern high-probability vs. random low-probability triplet) and Period (1–3) as within-subjects factors on the RTs, the mean amplitude of the CNV, and the mean amplitudes of the P3 peak and the late P3. In all ANOVAs, the Greenhouse-Geisser epsilon (ε) correction (Greenhouse & Geisser, 1959) was used when necessary. Original *df* values and corrected *p* values (if applicable) are reported together with partial eta-squared (η_p^2) as the measure of effect size. LSD (Least Significant Difference) tests for pairwise comparisons were used to control for Type I error.

Table 1. Mean percentage (%) and standard deviation of response accuracy split by triplet type and period.

	Pattern High	Random Low
	M (*SD*)	*M* (*SD*)
$Period_1$	96.0 (2.8)	95.8 (3.0)
$Period_2$	95.9 (2.8)	95.6 (2.5)
$Period_3$	95.8 (2.6)	95.1 (3.2)
Overall	95.9 (2.5)	95.5 (2.6)

Results

Behavioral results

The Type (pattern high-probability vs. random low-probability triplet) by Period (1–3) ANOVA on the RTs revealed a significant main effect of Type, $F(1, 35) = 8.86$, $p = .005$, $\eta_p^2 = .202$, indicating faster RTs on pattern high-probability triplets than on random low-probability ones (362.3 ms vs. 364.3 ms; see Fig. 2A). Although the Type * Period interaction was only a tendency, $F(2, 70) = 2.42$, $p = .096$, $\eta_p^2 = .065$, pairwise comparisons showed that the difference between pattern high-probability and random low-probability triplets was significant in $period_3$ (3.5 ms, $p = .004$) but not before ($period_1$: 1.4 ms, $p = .144$, $period_2$: 1.0 ms, $p = .217$). In addition, this difference was significantly larger in $period_3$ than in $period_2$ ($p = .026$; other pairwise differences were nonsignificant, $p \geq .136$). In details, RTs on pattern high-probability triplets tended to become faster as the task progressed ($period_3$ vs. $period_1$: 360.4 ms vs. 364.7 ms, $p = .052$); meanwhile, the fastest RTs on low-probability triplets were found in $period_2$ ($period_2$ vs. $period_1$: 362.7 ms vs. 366.1 ms, $p = .028$; other pairwise differences did not approach significance for both triplet types, $p \geq .120$). General skills did not reliably improve: The Period main effect was only a tendency, $F(2, 70) = 2.39$, $p = .099$, $\eta_p^2 = .064$, and, according to the pairwise comparisons, improvement between $period_1$ and

period$_2$ just reached significance (365.4 ms vs. 362.2, p = .050) and no further change was observed ($ps \geq .113$). Overall, RTs differed between the triplet types and some indication was found for the stabilization of this difference by the end of the task.

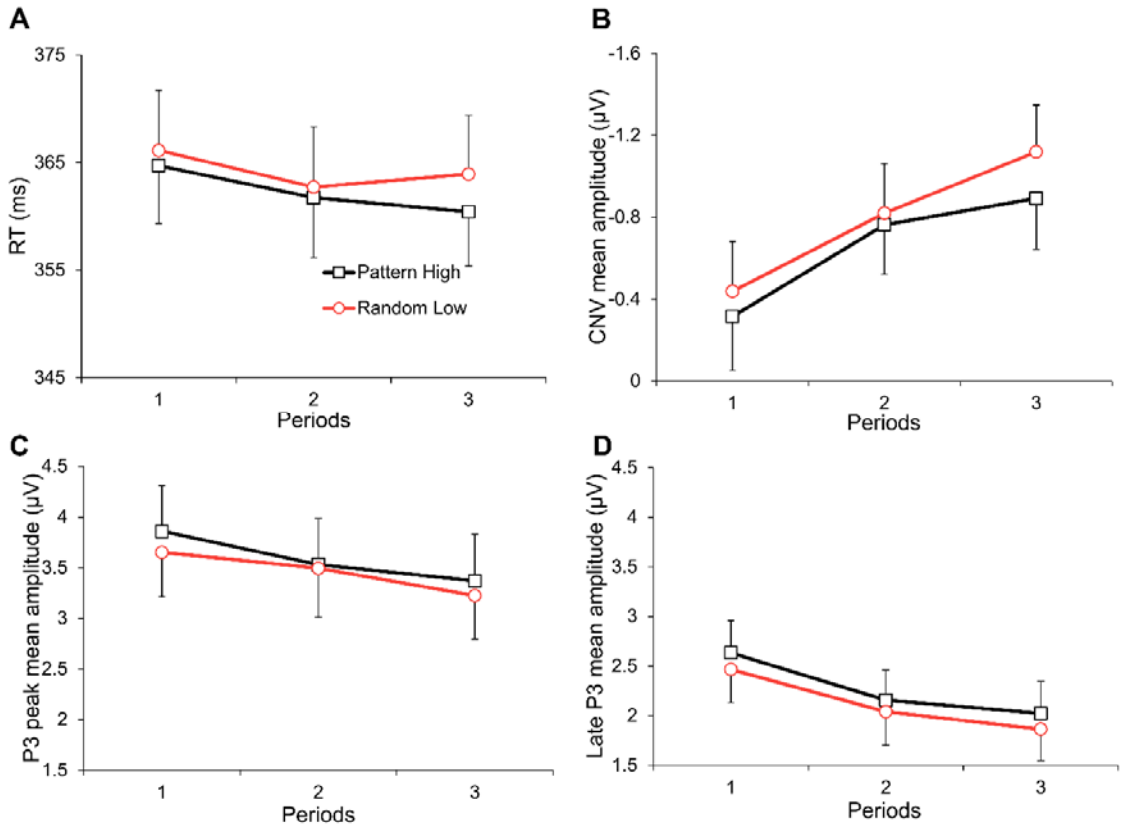

Figure 2. Group-average (A) RTs of correctly responded trials as a function of period (1–3) and triplet type (pattern high-probability vs. random low-probability triplets). Group-average (B) CNV, (C) P3 peak, and (D) late P3 mean amplitudes as a function of period and triplet type. Error bars denote standard error of mean.

ERP results

Grand average ERP waveforms for the two triplet types averaged for all epochs and split by period over the centroparietal electrode pool are presented in Figures 3-4, respectively.

CNV. The Type by Period ANOVA on the CNV showed a significant main effect of Type, $F(1, 35) = 10.46$, $p = .003$, $\eta_p^2 = .230$, indicating that the mean amplitude of the CNV was larger (more negative) for random low-probability triplets than for pattern high-

probability ones (-0.79 μV vs. -0.66 μV; see Fig. 2B and Fig. 3B, C). This difference did not change with practice (nonsignificant Type * Period interaction, $F(2, 70) = 2.07$, $p = .135$, $\eta_p^2 = .056$; see Fig. 4A, B). Meanwhile, as shown by the significant Period main effect, $F(2, 70) = 14.04$, $\varepsilon = .726$, $p < .001$, $\eta_p^2 = .286$, the overall CNV amplitude gradually increased as the task progressed ($period_1$: -0.38 μV, $period_2$: -0.79 μV, $period_3$: -1.01 μV; all pairwise differences were significant at $p \leq .013$; see Fig. 4A).

P3 peak. The Type by Period ANOVA on the P3 peak showed a significant main effect of Type, $F(1, 35) = 10.45$, $p = .003$, $\eta_p^2 = .230$, indicating that the P3 peak amplitude was lower for random low-probability triplets than for pattern high-probability ones (3.46 μV vs. 3.59 μV; see Fig. 2C and Fig. 3B, C). This difference did not change with practice (nonsignificant Type * Period interaction, $F(2, 70) = 1.20$, $p = .309$, $\eta_p^2 = .033$; see Fig 4A, B). The significant Period main effect, $F(2, 70) = 4.82$, $\varepsilon = .709$, $p = .021$, $\eta_p^2 = .121$, showed that the overall P3 peak amplitude decreased as the task progressed ($period_1$: 3.76 μV, $period_2$: 3.51 μV, $period_3$: 3.30 μV; $period_1 > period_3$, $p = .019$, $period_2 > period_3$, $p = .044$; see Fig. 4A).

Late P3. Similar results emerged for the late P3 from the Type by Period ANOVA. The mean amplitude of the late P3 was lower for random low-probability triplets than for pattern high-probability ones (significant main effect of Type, $F(1, 35) = 10.78$, $p = .002$, $\eta_p^2 = .235$; 2.13 μV vs. 2.27 μV; see Fig. 2D and Fig 3B, C), and, irrespective of the triplet type, the overall mean amplitude of the late P3 decreased with practice (significant main effect of Period, $F(2, 70) = 12.73$, $\varepsilon = .802$, $p < .001$, $\eta_p^2 = .267$; $period_1$: 2.55 μV, $period_2$: 2.10 μV, $period_3$: 1.94 μV; $period_1 > period_2$, $p = .001$, $period_1 > period_3$, $p < .001$; see Fig 4A). The Type * Period interaction was nonsignificant, $F(2, 70) = 0.11$, $p = .893$, $\eta_p^2 = .003$ (see Fig. 4A, B).

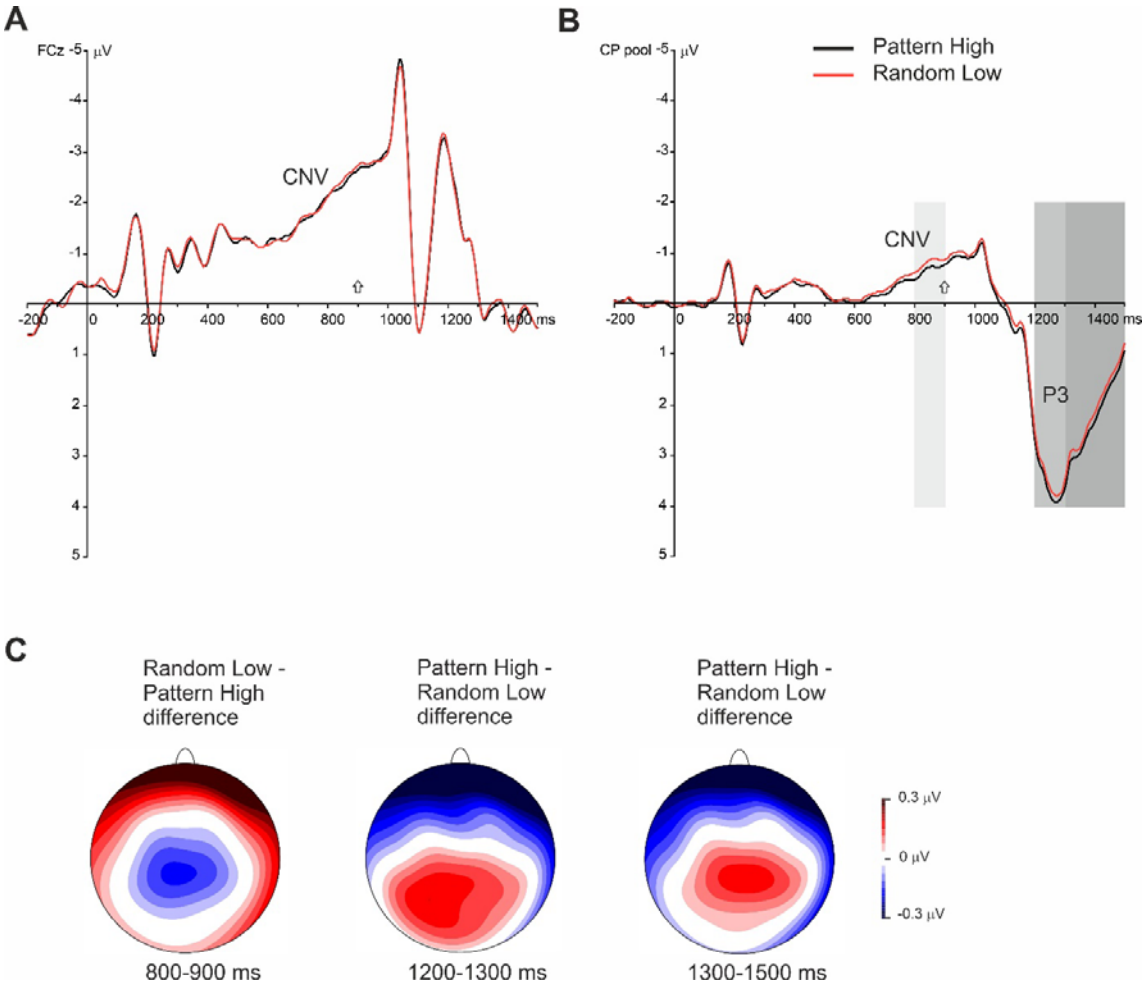

Figure 3. Grand average ERP waveforms at (A) electrode FCz and over (B) the centroparietal electrode pool are presented, displaying the CNV and the P3 components for pattern high-probability and random low-probability triplets, averaged for all epochs. The cue onset was at 0 ms, the target onset was at 900 ms; the latter is denoted by small arrows above the horizontal axes. In part (B) of this figure, the light-grey shaded area indicates the time window in which the CNV was quantified (800-900 ms), the medium-grey shaded area indicates the time window in which the P3 peak was quantified (1200-1300 ms), and the dark-grey shaded area indicates the time window in which the late P3 was quantified (1300-1500 ms). Negativity is plotted upwards here and in Figure 4. (C) The scalp topography (amplitude distribution) of ERP differences for random low-probability minus pattern high-probability triplets and for pattern high-probability minus random low-probability triplets in the time windows of the CNV, the P3 peak, and the late P3, respectively (from left to right), averaged for all epochs.

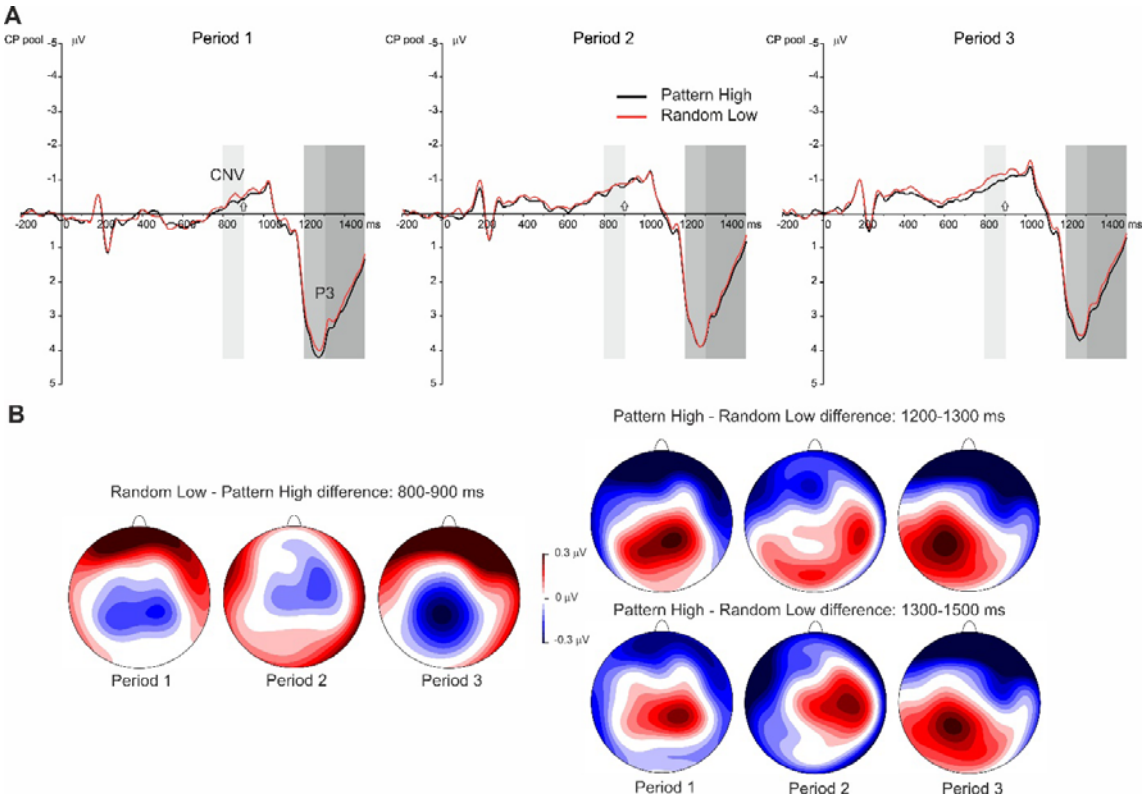

Figure 4. (A) Grand average ERP waveforms over the centroparietal electrode pool are presented, displaying the CNV and the P3 components for each period (1–3) and triplet type (pattern high-probability and random low-probability triplets). The cue onset was at 0 ms, the target onset was at 900 ms; the latter is denoted by small arrows above the horizontal axes. The light-grey shaded area indicates the time window in which the CNV was quantified (800-900 ms), the medium-grey shaded area is the time window of the P3 peak (1200-1300 ms), and the dark-grey shaded area is the time window of the late P3 (1300-1500 ms). (B) The scalp topography (amplitude distribution) of ERP differences in each period for random low-probability minus pattern high probability triplets in the time window of the CNV (left panel), and for pattern high-probability minus random low-probability triplets in the time windows of the P3 peak (right panel, top tow) and the late P3 (right panel, bottom row).

Discussion

This study provided ERP evidence for the operation of implicit anticipatory processes during the acquisition of probabilistic regularities. The CNV developed from the onset of the uninformative cue until the presentation of the target and its amplitude was larger before the

unpredictable than before the predictable target stimuli. This ERP difference reflecting sensitivity to the underlying regularities was continuously present with the same magnitude in the time window of target processing, indicated by the amplitudes of the P3 peak and the late P3 being lower for unpredictable than for predictable targets. As expected, anticipatory processing was shown not only by the CNV but also by the RTs that were faster to predictable targets. Based on these results, we propose that internal models have been implicitly formed on the probabilistic regularities of the stimulus stream. These internal models could have guided a series of anticipatory and preparatory processes that eventually facilitated stimulus processing.

Behavioral evidence accumulated so far indicates that participants respond overall faster or increasingly faster to high-probability triplets than to low-probability ones in the ASRT task (e.g., Janacsek et al., 2015; Kóbor et al., 2017; Nemeth et al., 2010; Nemeth, Janacsek, Polner, et al., 2013; Szegedi-Hallgató et al., 2019; Takács et al., 2017; Tóth et al., 2017). Faster responses specifically to pattern high-probability triplets than to random low-probability ones were also observed in implicit and explicit task versions without using warning cues (Horváth et al., under review; Kóbor, Horváth, Kardos, Takács, et al., 2019; Kóbor et al., 2018; Nemeth, Janacsek, & Fiser, 2013; Szegedi-Hallgató et al., 2019). The present task was a relatively slow-paced version: Participants had plenty of time (900 ms) to prepare their responses and their performance reflected high accuracy. Even this way, RTs differed between pattern high-probability and random low-probability triplets (cf. Vékony et al., 2019). This is in line with previous behavioral (cf. Juhasz et al., 2019; Szegedi-Hallgató et al., 2019; Török, Janacsek, Nagy, Orbán, & Nemeth, 2017) and ERP results (Kóbor, Horváth, Kardos, Takács, et al., 2019; Kóbor et al., 2018), proposing that the sensitivity to multiple probabilistic regularities has possibly been grounded in the implicit extraction of the triplet-level probability structure.

As in the present study, larger CNV for unpredictable vs. predictable visual stimuli was found previously during the implicit acquisition of probabilistic relations (Rose et al., 2001). Meanwhile, studies involving more easily learnable sequences of auditory stimuli (Jongsma et al., 2006; Stadler et al., 2006) and those that contrasted predictive auditory contexts with random ones in explicit experimental settings (Fogelson et al., 2009) showed the opposite. However, in those studies, repeating predictor/standard–target sequences were used. These sequences differ from the one we applied in the present implicit ASRT task version: Here, a stream of perceptually identical, task-relevant targets that all require keypresses create the ongoing stimulus context, and the exact directions of the targets are determined only by the underlying regularity. In our view, the processes reflected by the CNV in our task are related to the pre-allocation of attentional resources and to response preparation in an implicit and nonconscious manner. We base this interpretation on the assumption that the random low-probability, unpredictable stimuli would be more complex to-be-responded targets than the pattern high-probability ones, as already observed at the behavioral level. Therefore, the CNV is also suggested to be an electrophysiological marker of uncertainty in the current setting.

The observed centroparietal distribution of the CNV difference between unpredictable and predictable targets seems to be reasonable considering the previous literature. The late phase of the CNV can be differentiated into further components (Brunia, 2003; Brunia, Hackley, van Boxtel, Kotani, & Ohgami, 2011; van Boxtel & Brunia, 1994). For instance, it has been suggested that the component related to motor preparation reflects two aspects of the parieto-frontal motor system: the maintenance of the stimulus-response (S–R) links and the activation of the hand-motor area (Verleger et al., 2000). Therefore, the late phase of the CNV might reflect the selection between different motor programs, which is related to the parietal part of the motor system. In addition, the late CNV has been found to be more centrally

distributed and involving a posterior cortical network in the case of perceptual-motor tasks (Brunia & Damen, 1988; De Kleine & Van der Lubbe, 2011; Gómez et al., 2003; Leynes et al., 1998). Accordingly, response preparation might have been the major constituent of the observed CNV wave in the present study.

However, beyond response preparation, implicit and nonconscious predictions were generated about the direction of the upcoming target (cf. Kóbor, Horváth, Kardos, Nemeth, et al., 2019; Kóbor, Horváth, Kardos, Takács, et al., 2019). Consequently, it is conceivable that the presentation of the target arrow per se served as a feedback about the “correctness” of these predictions (i.e., whether the targets were anticipated outcomes or not). Therefore, the late CNV could have also consisted of the stimulus-preceding negativity (SPN) reflecting anticipatory attention to the perceptual informational delivered by the target, which might additionally contribute to the more posterior scalp distribution of the difference (Brunia et al., 2011; Hackley et al., 2014; van Boxtel & Brunia, 1994).

We intended to measure the genuine predictability of the trials as a result of acquiring the probability structure of the task. To this end, a simple fixation cross was used as an uninformative cue stimulus, which is somewhat unusual in cued RT tasks (but see Boehm et al., 2014; Pauletti et al., 2014). The fixation cross did not contain probability or direction information about the upcoming target, it only served a warning function. Since no information was delivered about which S–R links should be selected before target presentation, a generic pre-activation of the sensory-motor areas might have been needed for fast and accurate responding (Pauletti et al., 2014). Similarly, sustained activity in the frontoparietal network mediating response selection (cf. Schumacher, Hendricks, & D'Esposito, 2005; Verleger et al., 2000) might have also been involved in task solving. Supporting this notion, the amplitude of the CNV was not only modulated as a function of target probability but it also increased as the task progressed in time, irrespective of

probability information. In our earlier study, when the pattern high-probability trials were perceptually distinguishable from the random trials (i.e., marked with different colors) and no other cues were used, proficiency in the task and response automatization for the former trials were evidenced by the decreasing amplitude of different ERP components (N2, P3, Ne, Horváth et al., under review; Kóbor et al., 2018). In contrast, since target probability was not explicitly denoted in the present experiment, and the task was perceived as increasingly exhausting according to verbal reports (not presented in the Results section), the probability-non-specific CNV amplitude enhancement likely indicates the growing effort participants needed to maintain task performance.

Although RTs became faster due to practice at the descriptive level, general skill improvements were not statistically significant over task periods. (Please, note that general skill improvements are independent of the observed RT difference between high- and low-probability triplets.) This, again, suggests that sustained effort might have been needed for stimulus processing and responding. As speed and accuracy were equally emphasized in the present experiment, it is unlikely that the CNV amplitude enhancement was associated with lower response caution and/or increased response speed (Boehm et al., 2014). To confirm this assumption, correlational analyses were performed to test the associations between RTs and accuracy and between each of these behavioral measures and the CNV amplitude quantified over the CP pool between 800 ms and 900 ms. These analyses were run for each triplet types separately in the corresponding time periods (e.g., RTs to random low-probability triplets in $period_2$ with CNV amplitude for random low-probability triplets in $period_2$) as well as for the entire acquisition phase (e.g., mean accuracy for pattern high-probability triplets with the mean amplitude of the CNV for pattern high-probability triplets). Since none of these correlations were significant (all ps $\geq .307$), the present data would rather not indicate speed-accuracy trade-off in task performance.

The differential ERP effect for predictable vs. unpredictable stimuli persisted in the time window of the P3 component with similar magnitude. Particularly, the enhanced ERP amplitudes before unpredictable target stimuli appeared as decreased amplitudes after target onset (cf. Killikelly & Szűcs, 2013). The P3 amplitude has long been suggested to scale the probability of the stimulus (Donchin, 1981; Donchin & Coles, 1988; Mars et al., 2008) and to be modulated by the acquisition of predictive relations embedded in the stimulus sequence (e.g., Batterink, Reber, Neville, & Paller, 2015; Eimer, Goschke, Schlaghecken, & Stürmer, 1996; Jost, Conway, Purdy, Walk, & Hendricks, 2015; Rüsseler, Münte, & Wiswede, 2018). Meanwhile, current theoretical accounts of this component suggest its more intricate functional relevance in decision making and in linking stimulus evaluation to response selection (Kelly & O'Connell, 2015; Twomey, Murphy, Kelly, & O'Connell, 2015; Verleger, Jaśkowski, & Wascher, 2005; Verleger & Śmigasiewicz, 2016). To propagate the latter, the CNV and the P3 can be interrelated, and, accordingly, the observed ERP variation in our study can be regarded as a "CNV return" to baseline and its "overshoot" into the positive direction (Verleger et al., 2013). To further support this concept, not only the ERP effect related to predictability persisted but also the time-on-task effect, i.e., the overall CNV enhancement, which appeared as decreasing P3 amplitudes as the task progressed.

The CNV amplitude modulation likely reflects the activation and maintenance of the S–R link relevant to the given target (Verleger et al., 2000). Similarly, in terms of the theoretical accounts of the P3, the concept of S–R link might also help explaining the P3 findings. According to this concept, S–R links established with practice during the task are reactivated for initiating the correct response, and the P3 reflects the amount of this reactivation process (e.g., Verleger, Hamann, Asanowicz, & Śmigasiewicz, 2015; Verleger et al., 2017). The implicit acquisition of the probability structure could change the S–R links related to unpredictable stimuli that might require stronger reactivation, yielding larger P3

amplitudes (cf. Kóbor, Horváth, Kardos, Takács, et al., 2019). However, due to the cued design, some of the stimulus processing might occur in an anticipatory manner. It is possible that the stronger response preparation before the unpredictable stimuli facilitates target processing that uses less attentional resources (Polich, 2007; Polich & Criado, 2006) and operates at a lower decision threshold (Kelly & O'Connell, 2015), eventually yielding *decreased* P3 amplitudes. At the same time, this facilitated processing is not reflected in the RTs, as those are still slower for unpredictable stimuli. The implicit, nonconscious aspect of the task, however, might explain this matter, since "implicit preparation" might be enough for responding correctly but not for responding as fast as to predictable targets. Nevertheless, this finding is also in line with the assumption that movement initiation and movement preparation could be independent processes (Haith, Pakpoor, & Krakauer, 2016).

To conclude, the behavioral and ERP markers of implicit anticipation differed between predictable and unpredictable events arranged in a sequence of visual stimuli. Although the warning signals were unspecific to the predictability of these target events, lengthened RTs together with enhanced CNV and attenuated P3 amplitudes were recorded for unpredictable as compared with predictable events. To explain these ERP amplitude modulations, we propose that, during the preparatory phase of processing, more resources were needed to maintain the stimulus-response contingencies appropriate for the unpredictable events. This pattern of results possibly emerged due to the incidental and implicit acquisition of the probabilistic regularities through the formation of internal models, which is fundamental not only in perceptual and response selection processes but also in learning and memory. In line with this interpretation, our results further suggest that the CNV, by reflecting the active operation of these internal models, could be considered as a neurocognitive marker of uncertainty. This ERP component would be useful in investigating the acquisition of probabilistic regularities in clinical and nonclinical samples.

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Disclosure of interest

The authors report no conflicts of interest.

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