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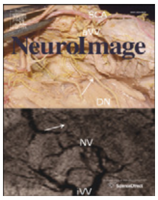

Full Length Articles

ERP evidence of adaptive changes in error processing and attentional control during rhythm synchronization learning

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ABSTRACT

The ability to detect and use information from errors is essential during the acquisition of new skills. There is now a wealth of evidence about the brain mechanisms involved in error processing. However, the extent to which those mechanisms are engaged during the acquisition of new motor skills remains elusive. Here we examined rhythm synchronization learning across 12 blocks of practice in musically naïve individuals and tracked changes in ERP signals associated with error-monitoring and error-awareness across distinct learning stages. Synchronization performance improved with practice, and performance improvements were accompanied by dynamic changes in ERP components related to error-monitoring and error-awareness. Early in learning, when performance was poor and the internal representations of the rhythms were weaker we observed a larger error-related negativity (ERN) following errors compared to later learning. The larger ERN during early learning likely results from greater conflict between competing motor responses, leading to greater engagement of medial–frontal conflict monitoring processes and attentional control. Later in learning, when performance had improved, we observed a smaller ERN accompanied by an enhancement of a centroparietal positive component resembling the P3. This centroparietal positive component was predictive of participant's performance accuracy, suggesting a relation between error saliency, error awareness and the consolidation of internal templates of the practiced rhythms. Moreover, we showed that during rhythm learning errors led to larger auditory evoked responses related to attention orientation which were triggered automatically and which were independent of the learning stage. The present study provides crucial new information about how the electrophysiological signatures related to error-monitoring and error-awareness change during the acquisition of new skills, extending previous work on error processing and cognitive control mechanisms to a more ecologically valid context.

Introduction

For most people synchronizing movement with a musical rhythm by dancing, clapping or tapping their feet is natural and requires no special effort. However, expert musical performance requires the production of complex rhythms that are mastered through practice. When learning a new piece, the musician first has to form an internal template of the temporal events of the rhythm to be able to plan and execute the correct sequence of movements (Pfordresher and Palmer, 2006; Pfordresher et al., 2007). Furthermore, these internal representations of the rhythm might be used to monitor the motor output and to track errors in order to improve performance. Early in learning, this template may be less well determined but with practice and feedback, it becomes more precise.

Error processing in humans is thought to be mediated by a system operating in the medial–frontal cortex (MFC) (Botvinick et al., 2001; Holroyd and Coles, 2002; Ridderinkhof et al., 2004). The contributions of this system during music performance have only recently begun to be explored. Behavioral and ERP studies have shown that musicians are able to plan several notes in advance (Pfordresher and Palmer, 2006; Pfordresher et al., 2007) and that they can detect upcoming errors even before the action is initiated or auditory feedback available (Maidhof et al., 2010; Ruiz et al., 2009). Thus it has been suggested that during skilled performance, error-monitoring does not rely on external feedback but is mainly guided by internal, feed-forward models of the motor plan (Desmurget and Grafton, 2000; Wolpert and Miall, 1996; Wolpert et al., 1995), which enables fast error-correction processes (Rabbitt, 1966; Rodriguez-Fornells et al., 2002).

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These studies have provided suggestive evidence about the possible engagement of error-monitoring mechanisms during skilled music performance, but they do not address how error processes might evolve during the acquisition of a new skill. To address this question we examined the process of learning musical rhythmic patterns in untrained individuals and measured changes in ERP signals associated with error-monitoring and error-awareness.

Studying error processing in the context of rhythm learning is particularly interesting for two reasons. First, while error-monitoring has been hypothesized to be related to skill acquisition (Adams, 1971; Palmer and Drake, 1997), to the best of our knowledge no previous ERP studies have examined how error-monitoring and error-awareness are influenced by learning during the acquisition of either musical and general motor skills. Second, the type of errors produced during skill learning differs from the type of errors studied in standard reaction time tasks (Eriksen and Eriksen, 1974) in which errors are categorical. During skill learning errors are often relative: the right response at the wrong time, or awkwardly performed. In addition, the perception of error commission, error-awareness, may depend on the accuracy of the internal representation of the action to be executed, and this representation changes with learning. Therefore we sought to examine possible changes in the error-monitoring and error-awareness systems with learning in a context that mirrors many situations in which we acquired new motor skills.

EEG studies examining performance on reaction time tasks have consistently shown that erroneous responses lead to an early negative component in frontocentral electrodes appearing immediately after error commission (within 0-100 *ms* after error onset), the error-related negativity (ERN) (Falkeinstein et al., 1990; Gehring et al., 1993). Evidence suggests that the ERN is generated in the MFC, specifically in the anterior cingulate cortex (ACC) and pre-SMA (Debener et al., 2005; Dehaene et al., 1994; Ullsperger et al., 2014a; Yeung et al., 2004), and reflects brain mechanisms sensitive to inappropriate action-sets and conflicting information. It has been proposed that the ERN may represent a neural signature of the implementation of top-down control mechanisms, such as the reallocation of attention or the adjustment of motor thresholds to promote post-error adaptions (Botvinick et al., 2001; Kerns et al., 2004; Marco-Pallares et al., 2008; Ridderinkhof et al., 2004). While the ERN may reflect a neural signal for fast and automatic processes of error-monitoring irrespective to the degree of error-awareness (Nieuwenhuis et al., 2001), conscious error perception has been associated to a slow and sustained centroparietal positive ERP response that occurs 300 to 500 ms after the error onset, the error-related positivity (Pe) (Murphy et al., 2012; Nieuwenhuis et al., 2001; O'Connell et al., 2007; Overbeek et al., 2005; Steinhauser and Yeung, 2010). Important, using principal components analysis (Arbel and Donchin, 2009) it has been shown that the Pe is composed of two different subcomponents: an early frontocentral component and a later centroparietal component which in terms of latency and scalp distribution resembles the P3b as a neural response to salient target stimuli in oddball tasks (Overbeek et al., 2005; Ridderinkhof et al., 2009). Evidence from signal detection theory (Hillyard et al., 1971; Woods et al., 1980) and, more recently, from the context of error detection (Murphy et al., 2012; Steinhauser and Yeung, 2010) and perceptual decision-making (O'Connell et al., 2012) support the idea that these centroparietal signals, the late Pe and the P3b, reflect common neural computations related with the accumulation of internal evidences leading to the awareness of actions and events motivationally relevant for on-going behavior, such as performance errors. Therefore the frontal ERN and later centroparietal positive components seem to index different aspects of error processing: error-monitoring and error-awareness.

Recent ERP studies in trained musicians performing well-learned pieces or scales (Maidhof et al, 2010; Ruiz et al., 2009) revealed a frontal negative component similar to the ERN, occurring right before the onset of erroneous responses (occurring approximately 30–100 ms before the error). This "pre-ERN" component was interpreted as a prediction error signal at the level of motor preparation. This pre-ERN signal is clearly distinguishable from other ERP responses related to movement preparation, such as the Readiness Potential (RP) (Shibasaki and Hallet, 2006) or the Lateralized RP (Gratton et al., 1988) in terms of its spatial distribution and latency. The observation of error-related signals in the MFC even before an error was committed suggests that error-monitoring during overlearned performance is implemented through neural feed-forward computations. Still we do not have clear evidence how error-monitoring processes are engaged during the acquisition of musical skills.

Nevertheless, although the error-monitoring system has not been formally studied during the acquisition of rhythm skills, previous neuroimaging studies have shown that medial–frontal structures of the brain associated with action monitoring, such as the ACC and pre-SMA, are particularly active during early stages of motor skill acquisition (Floyer-Lea and Matthews, 2005; Jenkins et al., 1994; Jueptner et al., 1997; Petersen et al., 1998; Ramnani and Passingham, 2001; Toni et al., 1998). The greater activity of these regions early in learning, when the task is more demanding and errors are more likely, probably reflects an increased engagement of the error-monitoring system tracking inappropriate response tendencies, monitoring competition between multiple conflicting motor plans and, consequently, signaling the need for increased attentional control (Botvinick et al., 2001; Jueptner et al., 1997; Paus et al., 1998).

Drawing on this background, we designed a novel experiment in which musically naïve individuals learned to reproduce a series of rhythmic patterns across 12 trials of learning, by synchronizing tapping movements with auditory events with different time (rhythmic) intervals. We hypothesized that during early learning, when internal representations of the rhythms were weak there would be greater response conflict and thus greater demand for cognitive control leading to an increase of the amplitude in the ERN component (Botvinick et al., 2001; Gehring and Fencisik, 2001; Yeung et al., 2004). In contrast, we predicted that later in learning there would be a decrease of the ERN reflecting less engagement of the error-monitoring system tracking performance conflicts and recruiting control. Furthermore, we predicted that as learning progresses and participants develop stronger internal representations of the different templates associated to the learned rhythms, they will be more certain about their performance and errors would become more salient. We expected that during rhythm learning the accumulation of internal evidences leading to error-awareness should be accompanied by an increase of later centroparietal positive components.

Methods

Participants

Eighteen students from the University of Barcelona (8 male, 10 female) between the ages of 19 and 31 (mean + SD = 21 ± 3 years old) participated in the study after giving informed written consent. All participants were right-handed, neurologically healthy and had normal hearing. Participants had no formal musical training besides the standard music classes at elementary school. Data from 3 participants were removed due to an excessive rejection rate of the EEG data (higher than 25%, see the methods below). Thus, 15 participants were included in the final behavioral and ERP analyses.

Rhythm synchronization learning task

In this task participants first listened to and then tapped in synchrony with 8 different auditory rhythmic sequences. Each rhythm was presented 13 times in a single block so that learning could be assessed. Rhythms were delivered through stereo headphones (Creative HQ-1300) at a comfortable intensity level. Participants tapped in synchrony with the index finger of their right hand on a computer mouse. Stimuli were presented and responses recorded using Presentation software (Neurobehavioral Systems) on a PC computer. Response triggers were sent on-line to the PC recording the EEG.

The rhythms used in this experiment were based on those used in several previous studies (Chen et al., 2008a, 2008b). Each rhythm consisted of 11 woodblock notes, each 200 ms in duration, with total duration of 6 seconds. The 11 notes composing the rhythms had the same pitch, though the temporal organization of the notes differed such that different rhythm patterns were created. The interval following each sound (note) varied such that five different musical durations (onset-to-onset) were created. Each rhythm contained: five eight notes (each 250 ms), three quarter notes (each 500 ms), one dotted quarter note (750 ms), one half note (1000 ms) and one dotted half note (1500 ms).

The experiment was divided into 8 blocks. In each block participants were trained on one of the 8 rhythms for 13 trials. Each learning trial included two conditions that always followed the same order: (1) *Listen*—participants were instructed to listen carefully to the rhythm without moving; and (2) *Synchronize*—participants were instructed to tap in synchrony with each sound in the rhythm and to avoid correcting their errors (Fig. 1). The beginning of each condition within each block was signaled by a warning tone 500 ms in advance. Between conditions there was 3.5 second pause for eye-blinking. Each block had duration of 9 minutes and on average the EEG session lasted 1.5 hours. Before the EEG session, participants were trained with 2 very basic rhythms to familiarize them with the task.

Behavioral analysis of rhythm synchronization performance

The first trial of each block was considered as a warm-up trial and excluded from the statistical analyses of both behavioral and ERP data. Rhythm production learning was assessed using three variables: (1) mean value of asynchrony (absolute value of the difference between the onset of each tap and the associated auditory tone in *ms*); (2) asynchrony variability (calculated as the SD of the asynchrony values), a measure related to performance consistency across learning (Wolpert et al., 2011); and (3) mean proportion of anticipated responses (taps that precede the onset of the auditory tones).

For the calculation of the mean asynchrony and asynchrony variability we compared the onset of participant's taps to the onset of each tone of the rhythm. We examined both anticipated and delayed (taps following the auditory tones) taps. If more than one tap fell within the same time interval, the first was taken and the second was excluded (Chen et al., 2008a). Furthermore, if one tap appeared right before and another right after the stimulus onset we considered the one with smaller asynchrony. Based on the visualization of the distribution of the responses in all individuals, we decided to exclude from the behavioral and ERP analysis all taps with an asynchrony greater than 260 ms (absolute value) because they were very infrequent, less than 3% of the total number of responses. Asynchrony values were averaged for each trial of learning and pooled across rhythms to obtain an average across trials 2–13 of learning (12 learning trials in total). The same procedure was applied for the mean proportion of anticipated responses.

The evolution of participants' performance throughout learning was tested using one-way ANOVAS comparing each of the dependent measures across the 12 learning trials [mean asynchrony (Fig. 2A), asynchrony variability (Fig. 2B) and the proportion of anticipated responses (Fig. 2C)]. For the purposes of linking behavioral performance with changes in ERP measures, we divided the learning trials into two periods: *early learning* (trials 2–5) and *late learning* (trials 10–13). Differences in performance between the two learning periods were assessed with paired *t*-tests for each variable.

Categorization of error and correct taps for the ERP analysis

During rhythm synchronization learning errors are relative, i.e. tap responses are more or less synchronous with the auditory stimuli. In this sense the perception of error commission relies on internal evaluations of the performer. As these evaluations may change over time with practice (while the performer consolidates his/her internal representations of the rhythm structure), the perception of error commission may follow the status of learning of the performer. For this reason, here we used a novel approach to categorize error responses in order to examine changes in EEG activity related to error-monitoring and error-awareness. Error and correct responses were categorized based on the distribution of the values of asynchrony of each participant's responses (anticipatory responses only, see the explanation below) during early (trials 2–5) and late (trials 10–13) learning stages separately. For each individual we took all his/her response asynchrony values and responses below the 50th percentile were categorized as correct (50% of responses with smaller values of asynchrony) and responses greater than the 75th percentile (the 25% of the responses with greater asynchrony) were categorized as errors (see examples from two representative participants at Fig. 2D).

Further, the number of anticipated error responses was matched across early and late learning conditions, such that there were not differences between the number of errors in early learning ($\text{mean} + \text{SD} = 45 + 5.6$; minimum: 37; maximum: 55) and late learning stages ($\text{mean} + \text{SD} = 46 + 6$; minimum: 38; maximum: 58) ($t(14) = 1.4$, $p > 0.05$) that could explain potential differences in the ERP results.

We chose to analyze only anticipatory responses because they were more common (65%) than the delayed responses. Besides, it was

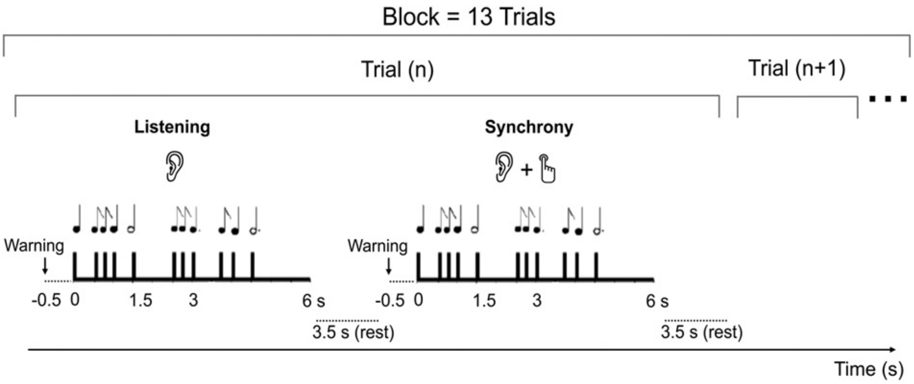

Fig. 1. (A) Schematic diagram of the task. Each trial comprises 2 different conditions that always follow the same order (listening, synchrony). After performing the 2 conditions participants move to the next trial. Each block includes 13 trials (the very first counts as a warm up trial). During one single block participants perform only one rhythm and the whole experiment involves 8 different rhythm sequences.

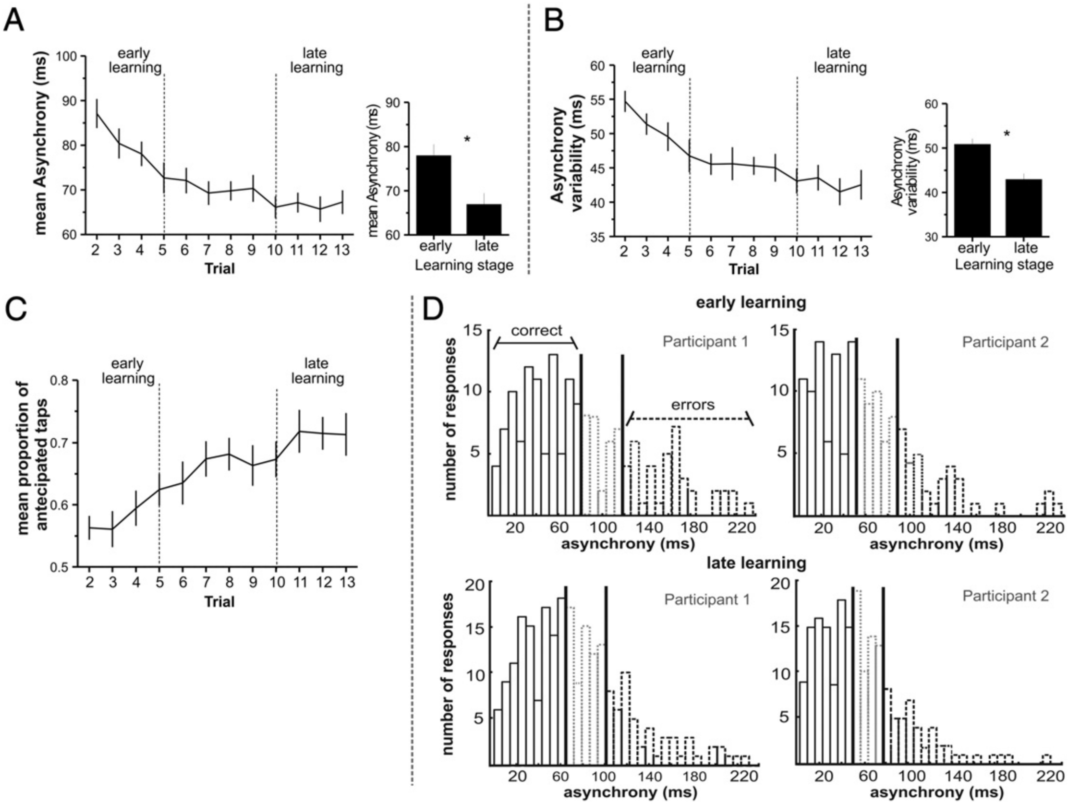

Fig. 2. (A) Average of the mean asynchrony (absolute value, ms) pooled across the 8 rhythms during all trials (trials 2–13) and t-test comparisons of the mean asynchrony between *early learning* (2–5 trials) and *late learning* (10–13 trials) stages. (B) Same as A regarding the asynchrony variability. Error bars represent SEM. **p*-value < 0.0001. (C) Average of the mean percentage of anticipated responses during the task (trials 2–13). (D) Graphic representation of the method used to categorize error and correct taps in two random participants. For each individual, 50% of the total number of anticipated responses with small values of asynchrony were grouped as correct taps (solid black bars), and the 25% of the total number of responses with larger values of asynchrony was classified as error taps (dashed black bars).

observed that after delayed responses the onset of ERP components associated with fast error processing mechanisms (e.g. ERN/Pe components) overlapped in time with ERP signals related with the processing of the auditory tones (e.g. the auditory N1 component). Thus, using only anticipated responses avoided confounds in the interpretation of the ERP data.

EEG recording and data analysis

EEG was recorded from tin electrodes mounted in an elastic cap located at 29 standard positions (Fp1/2, Fz, F7/8, F3/4, Fc1/2 Fc5/6, Fcz, Cz, C3/4, T3/4, Cp1/2, Cp5/6, Pz, P3/4, T5/6, PO1/2, Oz). Vertical eye movements were monitored with an electrode at the infraorbital ridge of the right eye. While performing the rhythms participants were instructed to fixate their eyes on a black square in the middle of the screen (gray background) in order to avoid eye movements. Between the listen and synchronize conditions there was 3.5 second pause for eye-blinking. Electrode impedances were kept below 5 kΩ. The electrophysiological signals were digitized at a rate of 250 Hz and filtered with online band-pass of 0.01–70 Hz (half-amplitude cutoffs). All scalp electrodes were referenced offline to the mean activity of the left and right mastoids.

Epochs of 1000 ms before and 1000 ms after the motor response (tap) were extracted from the EEG and baseline was corrected from −200 to −50 ms prior the response onset (response-locked ERP analysis). ERPs associated with the processing of the auditory tones composing the rhythms were also computed on epochs of 700 ms starting 100 ms before the onset of auditory tones; baseline was calculated from −50 to 50 ms to minimize misalignments of the waveforms based on anticipatory neural activity (Lange, 2011) and to overcome problems in baseline shifts due to the ERP deflections following the motor response. Trials exceeding ± 80 μV in both EEG and EOG during the epoch window were rejected offline. Only epochs that were preceded by at least 800 ms of error-free responses were entered in the analysis (Ruiz et al., 2009). EEG was offline low-pass filtered at <14 Hz for both response-locked and stimulus-locked ERP analysis. The data were further filtered with a band pass filter [3–9 Hz] in order to isolate theta-band specific ERPs associated with error and conflict monitoring (Cavanagh et al., 2012; Luu and Tucker, 2001). This method is also valuable to remove positive slow wave potentials in which error-related negative ERPs developed and stabilize possible drifts (Rodriguez-Fornells et al., 2002).

Analysis of ERP components locked to the motor response

The analysis of the grand-average ERPs following the motor response showed that error taps were followed by a cascade of different ERP components that developed during four distinct time windows (Fig. 3). Right after the response onset an ERN was observed in error taps. The ERN was followed by the early Pe component (Arbel and Donchin, 2009; O'Connell et al., 2007). In turn, the ERN and the early Pe components gave rise to another two ERP deflections, respectively labeled as the N1/auditory-feedback negativity (AFN) component and the centroparietal P3 component. As the N1/AFN developed around the onset of the auditory tones composing the rhythm sequences, we questioned whether this component would be linked to auditory evoked activity, actually representing the standard auditory N1 component (Hillyard et al., 1973; Woldorff et al., 1993) and, therefore, dissociated from the motor output process (i.e. ERN/Pe). To answer to this

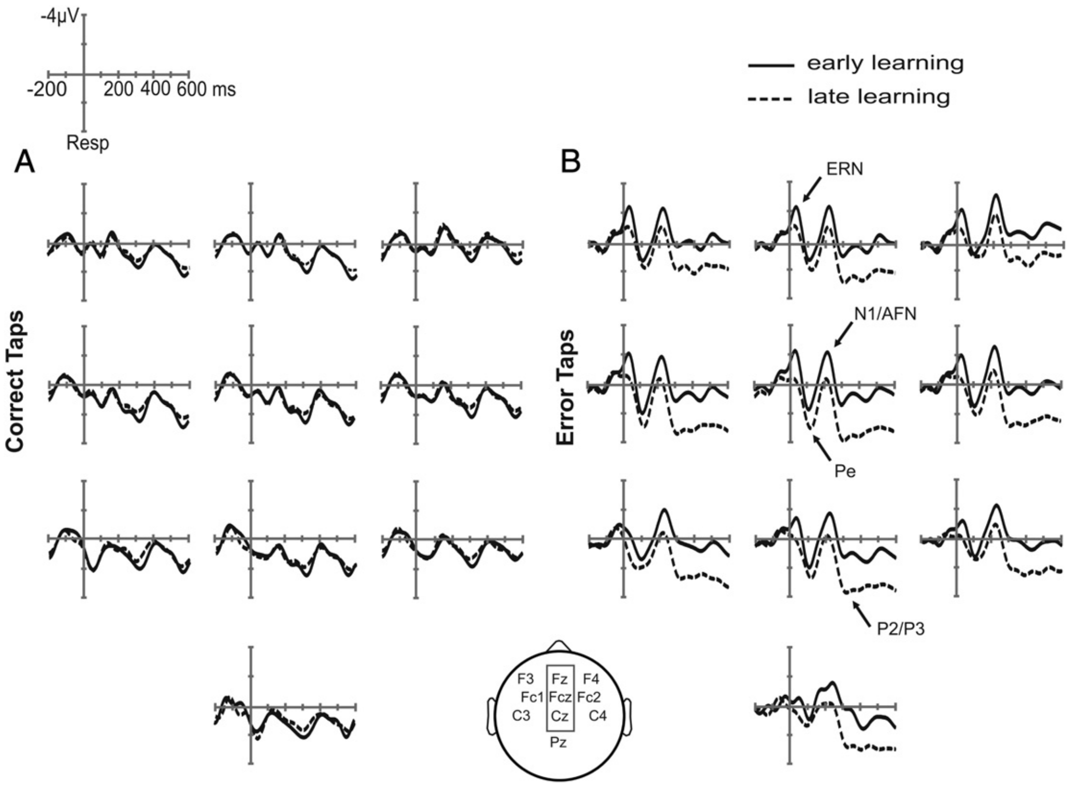

Fig. 3. ERPs response-locked to the motor responses made in anticipation to the auditory tones during *early learning* (solid line) and *late learning* (dashed line) stages for correct (left panel, A) and error (right panel, B) taps.

question single-trial ERPs analysis was additionally conducted (see for a similar approach Burle et al., 2008; Delorme and Makeig, 2004; Jung et al., 2001) as well as stimulus-locked ERP analysis (see below).

The inspection of single-trial ERPs was also critical to validate our approach to categorize correct and error taps. This analysis allowed us to inspect the EEG signal without averaging and, therefore, examine transient changes of the signal as function of the asynchrony variability (our measure to discriminate error from correct taps in all participants) (Burle et al., 2008; Jung et al., 2001).

Single-trial ERP epochs were analyzed from the EEG filtered data (low-pass <14 Hz) in the electrode Fcz (fronto-central scalp location), which is commonly used in ERP analysis of error processing. In Fig. 4

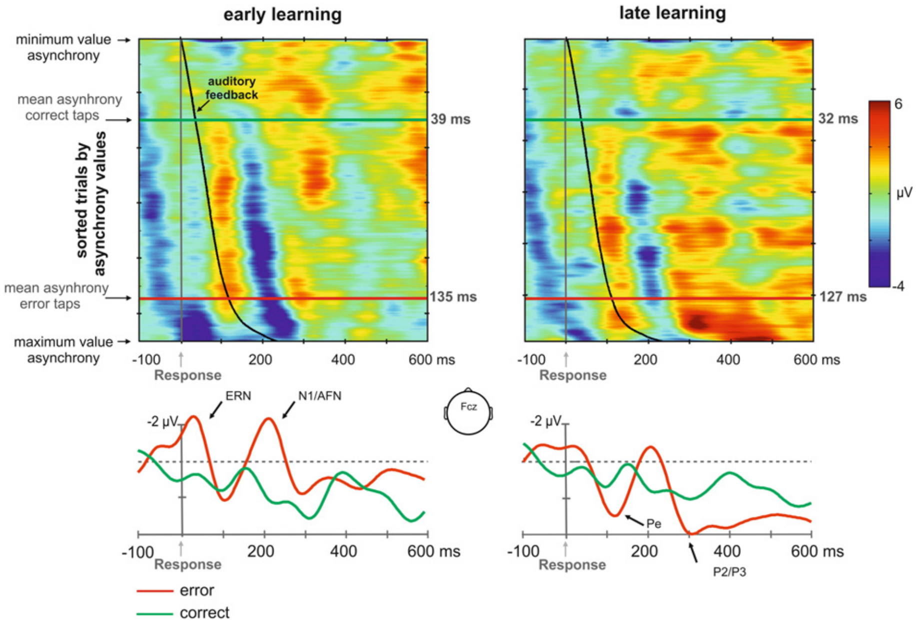

Fig. 4. Representation of single-trial ERPs containing all trials (all participants) at Fcz electrode for the *early* and *late learning* blocks. y-Axis represents single trials sorted by the absolute value of asynchrony, and x-axis represents the time respect to the response onset. The color represents the intensity of the signal for each time point and trial. The response onset time is indicated by the *gray vertical line* and the absolute value of asynchrony for a single trial (auditory feedback onset) is represented by the *oblique black line*. The mean value of asynchrony for error (*red line*) and correct (*green line*) taps in both learning stages is also indicated. In the bottom of the figure are plotted the grand average response-locked ERPs of all error and correct taps.

we depict single-trial ERPs as a color-coded map in which color-changing values reflect the intensity of the EEG signal recorded at a certain electrode location (Fcz), for a given trial and time point. Single-trials were sorted by decreasing values of asynchrony (y-axis), in order to explore ERP differences between small and larger values of asynchrony and displayed after smoothing with a narrow of 200 points moving window to increase the salience of stimulus and response locked features (Jung et al., 2001). Differences in the intensity of the signal are represented as dark blue (negative voltage polarity) and yellow-orange (positive voltage polarity) color activations. In all plots the response onset time (*gray vertical line*) and the absolute value of asynchrony at all single trials, that is, the moment of the auditory feedback presentation (*oblique black line*) are represented.

Time-windows for the statistical analysis of response-locked ERPs were chosen by the visual inspection of the grand-average waveforms (Figs. 3 and 5). Four time windows were selected: (0–50 ms, ERN); (90–150 ms, Pe); (180–250 ms, N1/AFN); and (300–450 ms, P3). The mean voltage of these four ERP components was subjected to ANOVAs with type of response (error, correct), learning stage (early learning, late learning) and electrode location (frontral, Fz; fronto-central, Fcz; and central, Cz) as within-subject factors. The Greenhouse–Geisser epsilon was used to correct possible violations of the sphericity assumption. p-Value after the correction is reported.

Analysis of ERP components locked to the auditory feedback

To tease apart the possibility that the error-related ERP effects observed for the N1/AFN and P3 components during the response-locked analysis were due to baseline problems resulting from the ERN/Pe deflection, stimulus-locked analysis was also conducted on error and correct taps for both learning periods (note that taps always preceded the auditory tones). Moreover this analysis allowed us to confirm that the onset of these two ERPs always followed the auditory tones

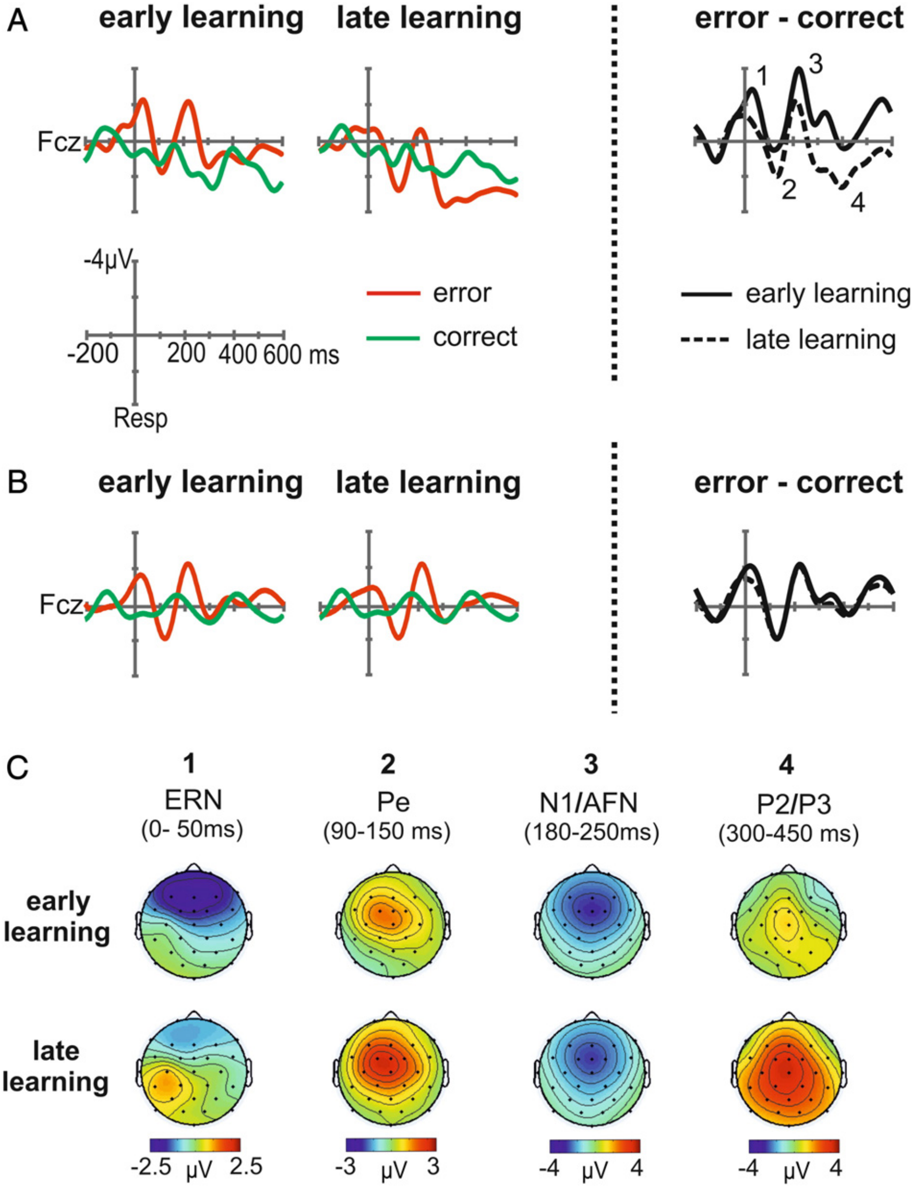

Fig. 5. ERPs response-locked to error (red) and correct (green) taps and for the difference waveform (error-correct) during *early learning* (solid line) and *late learning* (dashed line). (A) Grand averages low-pass filtered <14 Hz. (B) Grand averages band pass filtered (theta range: 3–9 Hz). (C) Topographical maps of the frontal ERN (1), the frontocentral Pe (2); the N1/AFN (3) and the centroparietal P2/P3 (4).

composing the rhythms (i.e. auditory feedback). ANOVAs with variables type of response (error, correct), learning stage (early learning, late learning) and electrode location (frontral, Fz; frontal-central, Fcz; and central, Cz) were computed on the mean voltage of these two components that developed following the onset of the auditory tones: the N1/AFN (80–120 ms) and the centroparietal P2/P3 (160–300 ms). Note that both the N1 and the P2/P3 signals from the stimulus-locked analysis reflect, respectively, the response-locked N1/AFN and P3 components. For heuristic proposes we labeled the ERPs from the stimulus-locked analysis as N1/AFN and centroparietal P2/P3 components. The Greenhouse–Geisser epsilon was used to correct possible violations of the sphericity assumption and p-value after the correction is reported.

Correlation analysis between behavior and ERP data

Furthermore we examined whether performance consistency, which was measured by the mean asynchrony and asynchrony variability throughout all learning trials, was correlated with neurophysiological responses that have been previously associated to error awareness, i.e. enhancement of centroparietal positive P3-like components (Murphy et al., 2012; Overbeek et al., 2005; Steinhauser and Yeung, 2010). We reasoned that more consistent or accurate performance might indirectly asses the accuracy of the internal representations built in relation to the target rhythm and that an increase in consistency might be related to larger P3 amplitude, the component associated to error awareness. To test this hypothesis, Pearson correlations between the mean value of asynchrony and asynchrony variability across all trials and the amplitude of the centroparietal P3 response (calculated by the difference error − correct taps across early and late learning stage) were computed.

Results

Behavioral performance during rhythm learning

Behavioral measures of performance showed significant improvements across the 12 trials of learning (Fig. 2) with decreases in mean asynchrony ($F(1,14) = 22.1$, $p < 0.001$); asynchrony variability ($F(1,14) = 55.2$, $p < 0.001$) and mean proportion anticipated responses ($F(1,14) = 55.9$, $p < 0.001$). For the purposes of comparison with the EEG data, learning was divided into early (trials 2–5) and late (trials 10–13) phases. Consistent with the results across all trials, comparison of performance across the two phases showed significant improvements for all three measures [mean asynchrony: early learning (mean ± SD), 77.8 ± 11 ms; late learning, 66.8 ± 10 ms: $t(14) = 4.8$, $p < 0.001$; asynchrony variability: early learning (mean ± SD), 50.6 ± 6 ms; late learning, 42.7 ± 6 ms: $t(14) = 6.4$, $p < 0.001$; mean proportion of anticipated responses: early learning (mean ± SD), 0.6 ± 0.1; late learning, 0.72 ± 0.1: $t(14) = 7.4$, $p < 0.001$].

The behavioral results showed that throughout the learning trials participants benefit from practice and improved their skill to tap more synchronized with the auditory tones composing the musical rhythms and with fewer fluctuations.

EEG signals of error-monitoring during rhythm learning

Error-monitoring based on the motor response (response-locked ERPs)

The inspection of the grand-average ERPs following the motor response revealed that error taps led to a cascade of four distinct ERP components (ERN, Pe, N1/AFN and P3) which were not observed in correct taps (Fig. 3).

The ERN was visible immediately after the production of an error (Figs. 3B and 5), peaking at about 0–50 ms. The ERN was also seen on the single-trial ERP analysis (Fig. 4) as a negative EEG signal starting right before the onset of the motor response (vertical gray line) and reaching maximal activity right after the response onset (notice the ERN peak in trials with larger values of asynchrony, as signaled by the red line representing the mean value of asynchrony in error taps). Typically, for the comparison between error and correct taps during early and late learning at the three midline recording sites (Fz, Fcz and Cz), the ERN was increased for error compared to correct taps (main effect of response type ($F(1,14) = 60$, $p < 0.001$) (Fig. 5A). The ERN showed a frontocentral topographical distribution with a maximum at the Fz site (Fig. 5C). An interaction response type × learning ($F(1,14) = 7.8$, $p < 0.05$) revealed that the ERN following errors was larger during early stages of rhythm learning when compared to the later learning period across all three recording sites (Figs. 3B and 5A; see also the single-trial analysis, Fig. 4). Next, the data were reanalyzed with a band pass filter [3–9 Hz] in order to isolate error-related theta-band specific ERPs (Cavanagh et al., 2012; Luu and Tucker, 2001) (Fig. 5B). Again a greater ERN after error taps (main effect of response type: $F(1,14) = 29.2$, $p < 0.0001$) was observed and especially during early stages of rhythm learning (response type × learning interaction: ($F(1,14) = 9$, $p < 0.01$) (Fig. 5B).

Following the ERN, around 90–150 ms, the Pe component was identified as an early positive deflection that was enhanced after error taps (main effect of response type: $F(1,14) = 6.2$, $p < 0.05$) (Fig. 3B and 5A). The early onset of this Pe and its frontocentral distribution (see on Fig. 5C the spatial map of this ERP) differentiates this Pe from the later centroparietal Pe which has been recently associated with error salience and consequent error-awareness (Arbel and Donchin, 2009; Murphy et al., 2012; O'Connell et al., 2007; Steinhauser and Yeung, 2010). Regarding the early Pe enhancement after error taps, no main effect of learning ($F(1,14) = 1.6$, $p > 0.05$) or its interaction with type of response ($F(1,14) = 3.6$, $p = 0.078$) was observed over the three recording sites.

Following the ERN/Pe components a second negative component was shown. As it can be seen in Fig. 4 (single-trial ERP analysis) this negativity, peaking at about 180–250 ms after response onset, developed along with the presentation of the auditory tones (highlighted by a dark oblique line). The computation of single-trial ERPs was critical to differentiate this ERP from the ERPs related with the motor response (ERN/Pe deflections). Note that this negativity appears ~100 ms after the auditory tones onset, which in terms of latency is very similar to the auditory N1 component (Hillyard et al., 1973; Woldorff et al., 1993). This negative component, termed N1/AFN, was increased in error taps compared with correct taps (main effect of response type: $F(1,14) = 77.0$, $p < 0.0001$) (Fig. 5a) with a maximum at Fcz electrode (response type × electrode interaction: $F(2,28) = 4.0$, $p < 0.05$) (see the fronto-central topographical distribution of the AFN on Fig. 5C). No learning effect was observed regarding this negative component ($F(1,14) < 1$) or the interaction response type × learning ($F < 1$). After applying a band pass filter in the theta band, which was crucial to remove the positive wave which this component developed (the early Pe), we confirmed the anterior findings by showing that the enhancement of the N1/AFN response after errors was not modulated by learning (both main effect of learning and the interaction type of response × learning were not significant ($F < 1$) (Fig. 5B).

Finally, both the grand-average waveforms and single-trial ERP analysis revealed that error taps during the late learning stage were associated with the increase of a later positive ERP occurring 300–500 ms after the error onset (the centroparietal P3). By looking carefully at Fig. 4 it can be seen that this positive ERP was greater in responses with larger values of asynchrony. This later positive response, representing the P3 component, showed a centroparietal distribution with a maximum at Cz electrode (Fig. 5C) and was marginally modulated by learning (main effect of learning: $F(1,14) = 4.1$, $p = 0.06$). A response type × learning interaction ($F(1,14) = 19.5$, $p < 0.001$) showed that this enhanced later centroparietal P3 for error taps was specific for later stages of learning (Figs. 3A and 5A).

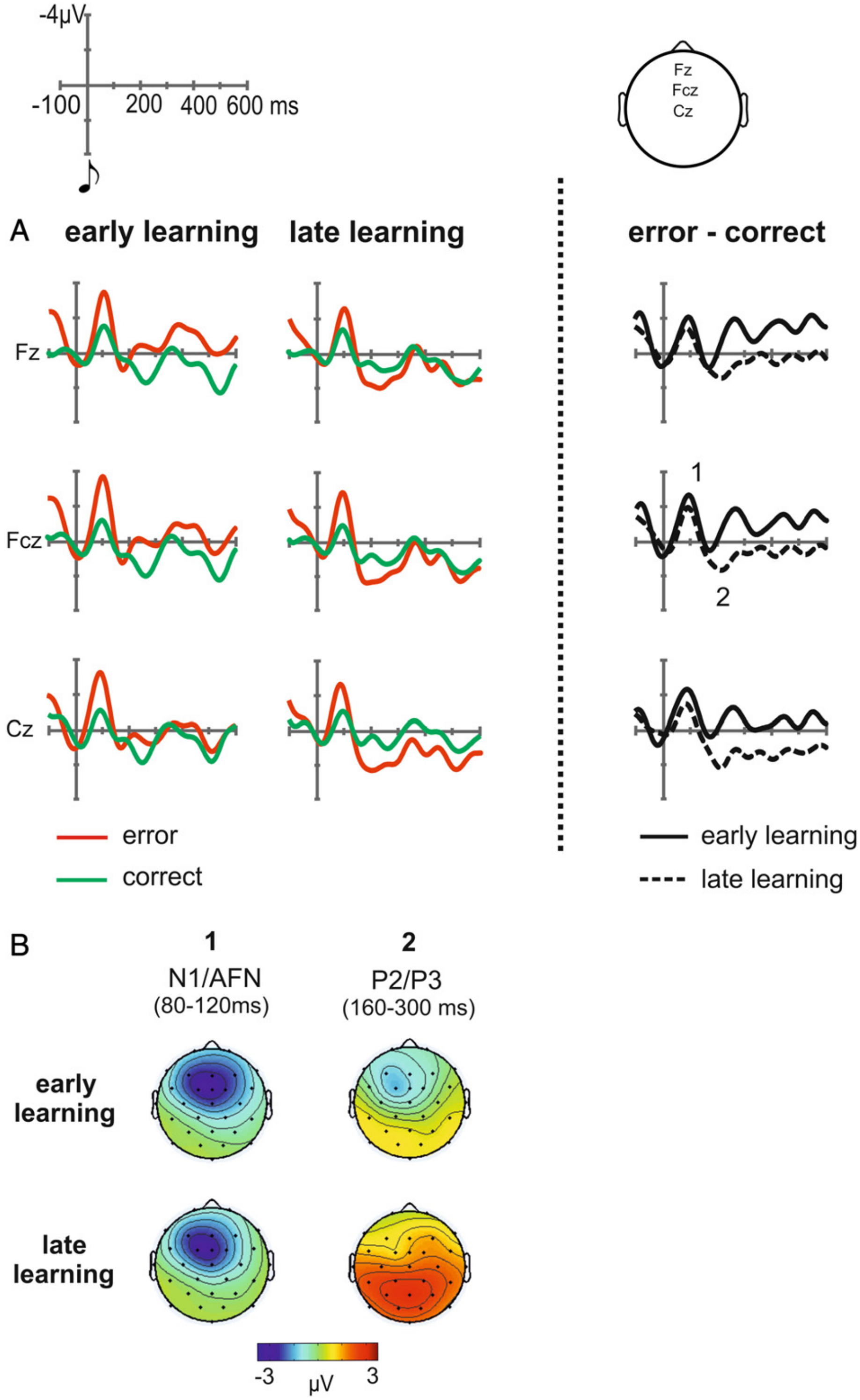

Fig. 6. (A) ERPs stimulus-locked to the auditory feedback (i.e. tones composing the rhythms) for error (red) and correct (green) taps and the difference waveform (error-correct) during *early learning* (solid line) and *late learning* (dashed line). (B) Topographical maps of error-related activity of the N1/AFN and centroparietal P2/P3components.

Error-monitoring based on auditory feedback processing (stimulus-locked ERPs)

The results from the stimulus-locked analysis (Fig. 6) replicated the findings regarding the N1/AFN and P3 modulations from the ERP analysis timed to the motor response.

Error taps compared with correct taps elicited an increased N1/AFN with maximal activation at Fcz location [main effect of response type: $F(1,14) = 14.2$, $p < 0.005$; and response type × electrode interaction: $F(1,14) = 16.8$, $p < 0.001$]. The N1/AFN peaked at about 100 ms after auditory stimulus onset as the classical N1 component. Note that the topographical distribution of the N1/AFN from the stimulus-locked analysis and the N1/AFN (response-locked analysis) after error taps is very similar; therefore the two ERPs may reflect the same neural mechanism. Alike the N1/AFN results from the response-locked analysis, no learning effect ($F(1,14) = 2.9$, $p > 0.05$) or the interaction between response type × learning

($F(1,14) = 2.7$, $p > 0.05$) was shown for the stimulus-locked N1/AFN component.

Moreover, the inspection of the ERPs associated with auditory feedback processing reconfirmed our previous result stating the specific increase of the centroparietal P3 component after error taps during the late learning stage. In error taps, after the N1/AFN response we observed a later centroparietal positive component which was modulated by Leaning ($F(1,14) = 6.3$, $p < 0.05$) and was enhanced during the late learning stage in all recording sites (response type × learning ($F(1,14) = 17.1$, $p < 0.005$). Notice that this centroparietal positivity (labeled as P2/P3 response) reflects the same component in both the response-locked and stimulus-locked cases as can be clearly observed when comparing their scalp distributions (see Figs. 5C and 6B).

Correlation analysis between performance accuracy and the late centroparietal positive component

We next examined whether whether individual performance consistency, which was measured by the mean asynchrony and asynchrony variability throughout all learning trials was associated with participants degree of error awareness, measured by enhanced activity in later centroparietal positive components. Participants with larger centroparietal P3 amplitude after erroneous taps reproduced the rhythmic sequences more synchronized with the tones (smaller values of asynchrony; $r = -0.66$, $p = 0.007$) and with less fluctuations (smaller values of asynchrony variability: $r = -0.58$, $p = 0.022$) during the whole task.

Discussion

In the present study, we tracked ERP changes associated with error-monitoring and error-awareness as musical untrained individuals learned to reproduce series of rhythmic patterns. Behavioral findings showed that across the learning trials participants improved in their ability to reproduce the rhythms and to synchronize their motor responses with the auditory stimuli. Changes in performance were paralleled by changes in cortical brain activity related to error-monitoring and error-awareness. The ERN amplitude was greater in early learning when compared to late learning, which indicates a greater involvement of the error-monitoring system when performance was more demanding and more cognitive control was required. It was also observed that in both stages of learning, erroneous compared to correct taps led to larger auditory evoked responses, indexed by the amplitude of the N1/AFN component, suggesting automatic attention orientation to the auditory tones after errors in performance. In agreement with our predictions, later in learning, errors were followed by a centroparietal P3-like component (the P2/P3) that was not present in the initial stages of learning. Importantly, we showed that the magnitude of this late centroparietal positive ERP was associated with individual differences in tap synchrony and asynchrony variability, suggesting a relationship between error-awareness and more accurate performance.

Error-monitoring and control mechanisms during early stages of rhythm learning

A key finding of our study was that the ERN was modulated by learning, showing greater amplitude in early compared to late learning. The ERN is hypothesized to represent a neural marker of error and conflict monitoring (Gehring et al., 1993; Holroyd and Coles, 2002; Yeung et al., 2004). Many studies have pointed the MFC, specifically the ACC and pre-SMA, as the source of the ERN (Debener et al., 2005; Dehaene et al., 1994; Yeung et al., 2004). The MFC is a key region for action monitoring and regulative aspects of motor and cognitive control, being critically involved in the flexible optimization of behavior and learning (Botvinick et al., 2004; Holroyd and Coles, 2002; Ridderinkhof et al., 2004; Ullsperger et al., 2014a,b).

The larger amplitude of the ERN during early stages of rhythm learning might reflect greater error-monitoring and response conflict experienced by the participants (Carter et al., 1998; Gehring and Fencisik, 2001; Yeung et al., 2004) as they tried to accurately reproduce the rhythm patterns when the representation of the appropriate response was as yet underdetermined (Botvinick et al., 2001). This finding points to a greater engagement of the MFC monitoring and conflict detection system (Botvinick et al., 2004; Nachev et al., 2007; Taylor et al., 2007) when performance was more challenging and more cognitive control and attention to the task was needed (Botvinick et al., 2001; Bush et al., 1998; Paus et al., 1998; Ramnani and Passingham, 2001). Early in learning the ERN may function as a signal to increase higher-level cognitive control to redirect attention to auditory feedback in order to overcome conflict among multiple possible motor plans (Botvinick et al., 2001; Kerns et al., 2004; Ridderinkhof et al., 2004). Conversely, as learning progresses and performance becomes less effortful and more automatized, the error-monitoring signal decreases. This decrease in error-monitoring might as well be associated to a diminished need to implement fast and very subtle error-correction processes, as less partial or full erroneous responses might exist. Thus, this decrease in error-monitoring activity might be associated to a reduced reliance on top-down control systems once performance becomes more fluent.

Considering that the ERN component has been associated with conflict and error processing in the MFC (Debener et al., 2005; Ridderinkhof et al., 2004; Holroyd and Coles, 2002; Botvinick et al., 2001) our results are in agreement with previous neuroimaging findings showing greater activation in medial prefrontal regions (specifically the ACC and pre-SMA) during the early stages of motor skill acquisition (Floyer-Lea and Matthews, 2005; Jenkins et al., 1994; Jueptner et al., 1997; Petersen et al., 1998; Ramnani and Passingham, 2001; Toni et al., 1998). Although error and conflict monitoring was not formally examined in those studies, it is very likely that the observed activations in the MFC were related to neural computations involved in the monitoring and compensation of a larger number of conflictive and error responses during the first stages of learning. Similarly, Brown et al. (2013) have recently evaluated pianists learning novel melodies. Improvements in performance with repetition were accompanied in this study by linear BOLD decreases in both the ACC and pre-SMA, which may indicate conflict resolution between multiple motor plans (*see* Nachev et al., 2007). In another study and using a different behavioral task (the Stroop task), it was observed that ACC activity related with response conflict diminished with practice (Bush et al., 1998). Importantly also, from animal studies, it has been observed that the ACC is a crucial region in rapid associative learning (Gabriel, 2002) and sequencing learning (Nakamura et al., 1998; Procyk et al., 2000).

Moreover, across both stages of learning, error taps were followed by larger auditory evoked responses (indexed by the amplitude of the N1/AFN component) compared to correct taps. Changes in the amplitude of the N1 could be associated with an attention orientation mechanism by which sensory processing in the auditory cortex is modulated (Hillyard et al., 1973; Woldorff et al., 1993). This finding is consistent with a previous study of audiomotor synchronization that also showed the modulation of the auditory N1 component in response to perturbations in the temporal organization of the auditory feedback and the resulting motor corrections (Praamstra et al., 2003).

Although speculative, it is probable that following errors the error-monitoring system may trigger changes in top-down attentional and motor control mechanisms that in turn modulate task-relevant sensory areas to promote post-error adaptations. The enhancement of auditory processing after errors is in line with recent fMRI evidences showing the modulation of task-relevant perceptual areas after errors via error-related medial frontal activity (Danielmeier et al., 2011; King et al., 2010). Importantly, however, our data indicate that attention orientation after errors is not modulated by learning. Thus for novice performers external feedback may be useful for post-error adjustments during all stages of skill acquisition. Although it has been proposed that auditory feedback is not crucial for error-monitoring in highly skilled performers (Maidhof et al., 2010; Ruiz et al., 2009), other evidence indicates that when auditory feedback is present performers still rely on the comparison between the auditory input and the motor output (Finney and Palmer, 2003; Pfordresher, 2006; Pfordresher and Palmer, 2006).

Error-awareness depends on the formation of internal templates of the target rhythm

The present study also revealed that during later learning errors were followed by a large centroparietal positive component (which was labeled as the P2/P3 component) appearing after the auditory feedback and which was not present early in learning. The latency and the topographical distribution of this centroparietal positive ERP resembles the late Pe and the P3b component (Arbel and Donchin, 2009; Ridderinkhof et al., 2009), which have been recently related to brain mechanisms associated to the conscious perception of errors or salient events in performance (Murphy et al., 2012; O'Connell et al., 2007; Ridderinkhof et al., 2009; Steinhauser and Yeung, 2010; Ullsperger et al., 2014b). Importantly, we did not observe any modulations of the early frontocentral Pe with learning that could suggest an association of this component with the subjective experience error awareness.

Although errors are very salient events, during early stages of learning error detection is accompanied by some degree of uncertainty. The increase of the centroparietal P3 late in learning may be evidence that an internal template of the rhythm structure has been established in working memory (Donchin and Coles, 1988) increasing participants' capacity to evaluate their response accuracy. In this sense, our findings are consistent with the idea that centroparietal P3-like signals reflect neural computations underlying the accumulation of perceptual evidences leading to the detection of salient events to performance (Hillyard et al., 1971; O'Connell et al., 2012) and, therefore, may be associated to the strengthening of internal evidence leading to error awareness (Steinhauser& Yeung, 2010).

Previous EEG studies on sequence learning have also described an association between centroparietal P3 signals and explicit knowledge about task rules (Baldwin and Kutas, 1997; Ferdinand et al., 2008). Further, professional musicians and conductors, who likely have strong internal models of expected sounds also exhibit larger amplitude of the P3 in response to deviant auditory stimuli when compared to music naïve subjects (Nager et al., 2003). The present results are also in agreement with previous studies showing the relevance of the P3 on the detection of violations in sequential patterns (Brochard et al., 2003; Ford and Hillyard, 1981; Nordby et al., 1988a, 1988b; Jongsma et al., 2004). For example, Jongsma et al. (2007) showed that the amplitude of the P3 component was sensitive to the ability of their participants to detect small tempo changes. Similarly, in a recent study, professional musicians showed shorter latency and increased amplitude in the P3 component when compared to non-musicians in a rhythm-change detection task (Ungan et al., 2013). Importantly, we showed that the magnitude of the centroparietal P3 was associated with individual differences in tap synchrony and asynchrony variability, suggesting a relationship between improved performance and error-awareness. These findings give empirical support to the idea that later centroparietal positive ERPs are positively related with learning on the basis of trial-and-error (Overbeek et al., 2005). In contrast, no relationship was found between the accurate performance and the amplitude of the ERN and performance. This is consistent with the idea that the ERN and later centroparietal positive ERPs reflect different aspects of error processing (Overbeek et al., 2005; Steinhauser and Yeung, 2010) that are differently affected by learning. Therefore, while the ERN may index more general and automatic monitoring processes (Nieuwenhuis et al., 2001) such as computing the degree of response conflict (Yeung et al., 2004), later centroparietal P3 signals may tap the subjective experience of error awareness.

Conclusion

The present results shed new light on how electrophysiological responses associated with error-monitoring and error-awareness are modified during the acquisition of new skills. Consistent with previous research we found that error-monitoring and error-awareness are partially dissociable processes in the human brain. During skill acquisition, error-monitoring processes indexed by the ERN were more engaged early in learning when the internal representation of the target response was underdetermined, conflict between competing motor responses was higher and greater recruitment of attentional control mechanisms was required. In contrast, error-awareness, identified by a late centroparietal P3 component, emerged only during later stages of learning, when the representation of the target rhythm was stronger and errors become more salient. Further, we extended previous findings by showing that during skill acquisition error-awareness is a byproduct of learning that likely relies on the consolidation of internal templates of the task and which is related to performance accuracy. Finally, the enhancement of the N1/AFN component after errors was consistent across both early and late learning, suggesting that in naïve participants errors trigger engagement of auditory attentional mechanisms that are automatic and independent of learning. We hypothesize that enhanced attention to auditory feedback following errors contributes to both error correction and the strengthening of the representation of the learned response. Overall, we think that this study is important in extending previous work on error processing mechanisms in simple reaction time tasks to more ecologically valid contexts involving learning of new skills.

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