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Contingent negative variation (CNV) associated with sensorimotor timing error correction

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Abstract

Introduction: Detection and subsequent correction of sensorimotor timing errors is fundamental to adaptive behavior. Using scalp-recorded event-related potentials (ERPs), we sought to find ERP components that are predictive of error correction performance during rhythmic movements.

Method: Healthy right-handed participants were asked to synchronize their finger taps to a regular tone sequence (every 600 ms), whilst EEG data were continuously recorded. Data from 15 participants were analyzed. Occasional irregularities were built into stimulus presentation timing: 90 ms before (advances: negative shift) or after (delays: positive shift) the expected time point. A tapping condition alternated with a listening condition in which identical stimulus sequence was presented but participants did not tap.

Results: Behavioral error correction was observed immediately following a shift, with a degree of over-correction with positive shifts. Our stimulus-locked ERP data analysis revealed, 1) increased auditory N1 amplitude for the positive shift condition and decreased auditory N1 modulation for the negative shift condition; and 2) a second enhanced negativity (N2) in the tapping positive condition, compared with the tapping negative condition. In response-locked epochs, we observed a CNV (contingent negative variation)-like negativity with earlier latency in the tapping negative condition compared with the tapping positive condition. This CNV-like negativity peaked at around the onset of subsequent tapping, with the earlier the peak, the better the error correction performance with the negative shifts while the later the peak, the better the error correction performance with the positive shifts.

Discussion: This study showed that the CNV-like negativity was associated with the error correction performance during our sensorimotor synchronization study. Auditory N1 and N2 were differentially involved in negative vs. positive error correction. However, we did not find evidence for their involvement in behavioral error correction. Overall, our study provides the basis from which further research on the role of the CNV in perceptual and motor timing can be developed.

Keyword: Error correction, Sensorimotor synchronization, Event-related potentials (ERPs), Contingent negative variation (CNV), Expectation, Timing

1. Introduction

Synchronized finger tapping to a rhythmic sequence of regular stimuli (sensorimotor synchronization, SMS) is a useful simple task to investigate anticipation and error correction processes in the context of repetitive movements (for comprehensive reviews on SMS studies, see Repp, 2005; Repp and Su, 2013). SMS tasks require the ability to control motor output based on *anticipation* of regular stimuli rather than *reaction* to them. As such, taps precede the stimulus onset by 20 to 80 milliseconds on average (termed as 'negative mean asynchrony' or NMA), in SMS paradigms where the stimuli are presented relatively 'fast' – (inter-onset interval below 2 seconds; Aschersleben, 2002; Mates, 1994a, 1994b). The NMA, which reflects anticipatory tapping behavior, is necessary for individuals to gain the subjective impression of tapping in synchrony with the stimuli (Aschersleben, 2002). The NMA serves as an index of performance during SMS tasks because it measures the individual's subjective perception of synchrony between tap and stimulus (Repp and Su, 2013).

Error correction, another characteristic phenomenon of SMS, is a dynamic process to sustain a consistent tap-stimulus relationship, and it occurs even when the pacing stimulus is regular because of inherent variability in the motor responses (Wing & Kristofferson, 1973a, 1973b). By introducing occasional time shifts in the regular stimulus presentation (a phase shift paradigm; Repp, 2000), the error correction process can further be investigated. For example, a phase shift is a local change in stimulus regularity, which leads the subsequent stimuli to be time-shifted from that point on, while maintaining an identical subsequent inter-onset-interval (IOI) (Repp, 2001b). Stimuli can either be shifted forward or backward in time relative to their expected onset. A negative shift brings the subsequent stimuli forward to an earlier time point (i.e., 'phase advance') due to a transient decrease in the inter-onset-interval. In contrast, a positive shift pushes the subsequent stimuli backward to a later time point (i.e., 'phase delay') due to a transient increase in the inter-onset-interval. Following such phase shifts, humans can rapidly adapt to the time-shifted stimulus sequence and return to their baseline NMA within several taps (i.e., phase error correction: hereafter termed ‘error correction’) (Repp, 2000, 2002). It has previously been shown that, with a relatively small phase shift (within about ±15% of the sequence inter-onset-interval), the compensatory error correction response is proportional to the size of the phase shift (Repp, 2002).

To understand the neural basis of error correction in the SMS tasks, we previously performed an fMRI study (Bijsterbosch *et al.*, 2011b). We have shown that bilateral frontal cortices, right inferior parietal cortex, and the left cerebellum were significantly activated in an SMS task with phase shifts, compared to an SMS task with regularly-paced stimuli. The neural mechanisms of error correction performance for negative and positive shifts in the stimulus presentation would likely to be different. For example, Repp (2002) showed that error correction performance for positive shifts was more variable than that of negative shifts. Furthermore, we have shown an over-correction for positive shifts as in previous studies (Praamstra *et al.*, 2003; Thaut *et al.*, 1998), whose degree was significantly less after practicing. By contrast, error correction of negative shifts was stable both during the testing sessions within a day, and during the testing sessions over a few days apart (Bijsterbosch *et al.*, 2011a).

Praamstra *et al.* (2003) explicitly sought to find ERP correlates of error correction to negative vs. positive shifts. In their study, participants were asked to synchronize their taps to a tone sequence with 500 ms inter-onset interval. Occasional shifts, or irregularities, were introduced (±15 ms or ±50 ms) to the tone sequence that was otherwise isochronous. They found a modulation of auditory N1 amplitude, possibly reflecting auditory attention: increased amplitude following the positive shifts but reduced amplitude after the negative shifts. Interestingly, the error-related negativity (ERN; Gehring *et al.*, 1990; Gehring *et al.*, 1993) in averaged ERPs occurred around 200 ms after a positive shift, with a current source located in the medial prefrontal cortex, but no ERN was identified after a negative shift. The ERN is an ERP component that appears after the execution of errors (Gehring *et al.*, 1990; Gehring *et al.*, 1993) and has been suggested to be associated with N2 (Praamstra *et al.*, 2003). Determining whether or not these ERP components reflect the error correction mechanism itself or are associated with post-error processing (i.e., conscious awareness of errors) requires further investigation.

One ERP component, the contingent negative variation (CNV), is associated with attention allocation in anticipation of an imperative stimulus to prepare a subsequent behavioral response with its peak exhibited around stimulus onset over the prefrontal cortex (i.e., type B CNV; Tecce, 1972). As such, the CNV would be associated with stimulus expectancy aspects of SMS. The ERP component is typically observed when two temporally-contingent events are separated by several seconds. However, an inter-onset interval between 0.5–1.5 s has also been shown to produce a robust CNV (Cui *et al.*, 2000). CNV peak latency has been closely related to an internal timing mechanism. For example, Macar and Vidal (2003) showed that when a current “to-be-timed” stimulus was longer than the previously-learned standard stimulus interval in a temporal generalization task, the CNV peaked at the offset time of the memorized standard stimulus, rather than at the offset of the current to-be-timed stimulus (for similar results, see Tarantino *et al.*, 2010). This result indicates that the CNV is a cerebral index of past experience of regularities such as internal temporal estimates.

The present study investigates whether the neural components associated with post-error processing (N1 and N2) or those related to expectation of subsequent stimuli following an error (CNV) would be a predictor of subsequent error correction performance. Stimulus-locked ERP waveforms were used to examine N1 and N2 in relation to ‘phase shift’ (negative vs. positive) and ‘movement’ (SMS vs. passive listening). To evaluate the impact of stimulus expectation following an error (CNV), we analyzed response-locked data to compare CNV in negative and positive SMS conditions. The passive listening condition (with the identical stimulus sequence as in the SMS conditions) was used to separate the impact of error correction from error detection.

We hypothesized that the expectancy-related neural component, CNV, would be related to the subsequent error correction performance.

2. Material and methods

2.1 Participants

Seventeen healthy volunteers participated. They were students from the University of Sheffield. Data from 15 participants were analyzed and reported here (5 males, mean age 21.79 years, SD = 5.83, range 18-38), because data from two participants were excluded due to excessive artifacts. All participants were right-handed, as assessed using the Edinburgh Handedness Inventory (Oldfield, 1971). After complete description of the study to the participants, written informed consent was obtained. This study was approved by the Department of Psychology Ethics Committee, University of Sheffield.

2.2 Stimuli and tasks

The auditory stimuli were 500 Hz square-wave tones of 50 ms duration. The tones were generated with Audacity software (http://audacityteam.org/) and presented binaurally via Harmon/Kardon HK395 speakers at an approximately 60 dB sound pressure level. E-prime software was used to control the experiment and record the event data, synchronized with the EEG recording (Schneider *et al.*, 2002). The tones were presented with an IOI of 600 ms based on the finding that an anticipatory response (i.e., negative mean asynchrony) could be obtained within the IOI range from 450 to 1,500 ms (Miyake *et al.*, 2004). While an IOI of 500 ms was utilized in Praamstra *et al.* (2003), we extended it to 600 ms to allow more time for CNV generation as 500 ms might not be enough for detailed CNV analyses (see Figure 7, Praamstra *et al.*, 2003). The tone sequence contained occasional phase shifts. The magnitude of the phase shifts was ±90 ms which was 15% of 600 ms. We used 15% because phase shifts within 2% to 15% of IOI would generate the error correction response that is proportional to the size of the phase shift (Repp, 2002). This phenomenon indicates that a single and relatively automatic error correction mechanism is involved within this phase shift range.

The task consisted of two conditions in 20 experimental blocks: 10 blocks of a tapping condition and 10 blocks of a passive listening condition. A tapping block alternated with a listening block. At the beginning of each block, 10 regular tones were presented to ensure that participants were familiar with the task. Following the first 10 tones, 15 tones for positive and 15 tones for negative shifts were presented in random order in a block, with a rule that shifts are separated by at least 7 regular tones. While the tone sequence was continuous during a block, we defined a trial as a sequence of 7 tones for data analysis purposes (*T-2*, *T-1*, *T0*, *T+1*, *T+2*, *T+3* and *T+4*), where *T0* was the tone at which the phase shift occurred and a new 600 ms sequence was introduced. In total, 150 trials were included for each shift condition.

Participants were seated in a comfortable chair in an acoustically shielded, dimly lit room. Each block was initiated as the participants pressed the start button. They were asked to close their eyes just before pressing the start button and keep their eyes closed, in order to minimize blink-related EEG artifacts and to limit a possible compounding effect of visually-evoked EEG responses by observing their finger movements (Barry *et al.*, 2007). Participants were informed of the random phase shifts and asked to tap in synchrony with the tone sequence while accommodating for occasional irregularities due to the phase shifts. Task instructions were given verbally between the blocks while they were also displayed on a 17- inch CRT monitor which refreshed at 75 Hz. Tapping was performed by pressing a response button with the right index finger. Participants rested between blocks. After each block, they were asked with the following questions in order to secure their attention to the task: a. whether they noticed any irregularities, b. if so, whether they could predict the time point of the phase shifts. All participants detected the irregularities in all blocks, but they could not predict the time point of the phase shifts. The experiment lasted approximately 1 hour.

2.3 EEG recordings and data analyses

EEG data were recorded with a 128-channel Geodesic Sensor Net (Electrical Geodesics, Inc., Eugene, OR), sampled at 500 Hz, and referenced to the vertex (Cz) with analog band-pass filter between 0.1 and 200 Hz. As recommended by the manufacturer, electrode impedances were kept below 50 kΩ. Vertical and horizontal eye movements were monitored with a subset of the recording channels.

The data were analyzed using the EEGLAB toolbox (http://sccn.ucsd.edu/eeglab/). The continuous data were first high-pass filtered (0.1 Hz) to minimize ERP onset time distortions (Acunzo *et al.*, 2012). We visually inspected all data and observed ‘bad’ channels were re-interpolated using spherical spline interpolation. We then obtained stimulus-locked and response-locked ERP epoch datasets. For stimulus-locked data analysis, data were segmented into stimulus-locked macro-epochs for each condition: listening negative (LN), listening positive (LP), tapping negative (TN), and tapping positive (TP), comprising tone positions from *T-2* to *T+4* (-0.3 s to 4.0 s, time-locked to *T-2*). We used the CleanLine toolbox to reduce line noise at 50 Hz (Mullen, 2012). To further minimize artifacts, the ADJUST toolbox was used. It operates upon implementation of independent component analysis (ICA) to automatically detect artifact independent components based on the artifact-specific spatial and temporal features (Mognon *et al.*, 2011). The data were then re-referenced to an average reference. A 20th-order low-pass filter with a 100 Hz cut-off and a Hamming window was applied to remove high frequency noise. The macro-epochs were subsequently segmented into shorter epochs, time-locked to the auditory stimulus (*T0*) and the preceding tone (*T-1*) for all conditions. The epochs were extracted comprising -100 ms to 600 ms, time-locked to stimulus presentation time (0 ms). We performed a baseline correction using the pre-stimulus interval from -50 ms to 0 ms (Praamstra *et al.*, 2003), by computing the average voltage during the pre-stimulus interval and subtracting this voltage from each time point in the epoch. Epochs greater than ±75 mV were rejected from the study.

Consequently, the data were averaged to form an ERP for each condition. Out of a total of 150 trials for each condition, the following number of trials were excluded across the 15 participants on average: LN: 15.60 (SD = 13.73), LP: 16.20 (SD = 15.03), TN: 18.07 (SD = 12.71), and TP: 18.20 (SD = 12.53).

For response-locked data analysis, from the continuous data (after high-pass filtering and bad channel interpolation), we extracted epochs time-locked to tap-onset, corresponding to the auditory stimulus (*T0*) and the preceding tone (*T-1*) for each condition: TN and TP. Otherwise, all data analysis steps were identical as stated above. The following number of trials were excluded out of a total of 150 trials for response-locked conditions: TN: 18.87 (SD = 13.77), and TP: 15.40 (SD = 10.04). Because epochs with a tapping response were occasionally absent, the number of trials for the response-locked analysis was smaller. However, the number of trials remained sufficient: TN: 125.53 (SD = 15.58), TP: 108.67 (SD = 17.64).

Condition-wise ERP averages were obtained from FCz, with topographic maps showing the scalp distributions of significant ERP effects. In our ERP analysis results, we applied the false discovery rate procedure (Benjamini & Hochberg, 2000) to *p*-values generated at each time-point to correct for multiple comparisons.

3. Results

3.1 Behavioral data

Figure 1 about here

Out of a total of 2,108 tones in the tapping condition, participants failed to respond to 14.70 % (SD = 5.12) of tones on average. Figure 1 shows averaged tap-tone asynchronies for sequences containing negative and positive shifts as a function of stimulus position (left panel) and the normalized error correction function (right panel). The normalized error correction function was used to directly compare the error correction performance between the negative and positive shift conditions. Firstly, we defined baseline performance as the average tap–tone asynchrony over trials from *T−4* to *T–1* for each condition. We then normalized the asynchrony values during *T0* to *T+4* to range from the baseline asynchrony 'zero' to the maximum shift at *T0* 'one', and the sign was removed (Praamstra *et al.*, 2003; Repp, 2000). The resulting normalized error correction functions were averaged across the trials in each condition. The normalized error correction functions were analyzed using a 2×4 repeated measures analysis of variance (ANOVA) with within-subjects variables, ShiftDirection (negative vs. positive shifts) and Position (*T+1*, *T+2*, *T+3*, *T+4*). Mauchly's Test of Sphericity showed that the assumption of sphericity had been violated for Position [W = .22, $\chi^2(5) = 19.18$, $p = .002$] and for the ShiftDirection*Position interaction [W = .03, $\chi^2(5) = 15.23$, $p = .01$]. Where sphericity could not be assumed, a Greenhouse-Geisser correction was applied, and reported hereafter. When multiple comparisons were made within our ANOVA analysis, Bonferroni-corrected *p*-values were reported in order to reduce the possibility of making a Type I error.

There was a significant interaction between ShiftDirection and Position on error correction [$F(3,42) = 10.00$, $p = .001$]. As can be seen in Figure 1 (right panel), the positive shifts were corrected significantly faster than the negative shifts at *T+1* [$p < .05$] but not at *T+2, T+3*, or *T+4*. In the tapping positive condition, the normalized asynchrony at *T+1* was not significantly different compared with *T+2*, *T+3*, and *T*+4 (also, no significant differences across *T+2*, *T+3*, and *T+4*). This indicates that the error correction occurred at *T+1* and that there was no further significant error correction in the subsequent taps in the tapping positive condition (as shown in Figure 1, right panel). In contrast, in the tapping negative condition, the normalized asynchrony at *T+1* was significantly higher than *T+2, T+3*, and *T+4* [all $p < .001$]. Moreover, the normalized asynchrony at *T+2* was significantly higher than *T+4* [$p < .05$]. This indicates that the error correction occurred through *T+1* and *T+2* in the tapping negative condition. There was a main effect of Position [$F(3,42) = 6.83$, $p < .01$], indicating that *T+1* was significantly higher than *T+4* [$p < .05$]. Furthermore, *T+1* was higher than *T+2* at a trend level of significance [$p = .072$]. The main effect of Direction was not significant [$F(1,14) = .89$, $p = .363$].

3.2 ERP data

3.2.1 Stimulus-locked data analyses

Figure 2 about here

Figure 2 shows grand averaged ERP waveforms for all experimental conditions at FCz site for illustration purposes only. Prior to the introduction of a phase shift, the morphology of the ERP waveforms was comparable in all conditions. After a phase shift, the waveforms mirrored their own stimulus presentation timing. As displayed in Figure 3, stimulus-locked ERP data were analyzed using a 2×2 repeated measures ANOVA with within-subjects variables of Condition (listening vs. tapping) and ShiftDirection (negative vs. positive). The shaded boxes in Figure 3 represent the significant time windows for the analysis of ERP magnitude: N1: 52-156 ms and N2: 262-364 ms. At 119 ms (see the first shaded box for N1 window), there was a significant interaction effect between Condition and ShiftDirection [$F(1,14) = 19.77$, $p < .001$]. Pairwise comparisons showed a significantly larger N1 amplitude in the tapping positive condition compared to the tapping negative condition [$p < .01$]. In contrast, the listening negative and the listening positive conditions were not significantly different. While there was a significant difference between the listening positive and the tapping positive conditions [$p < .05$], no significant difference was found between the listening negative and the tapping negative conditions. A main effect of ShiftDirection was observed [$F(1,14) = 31.75$, $p < .001$], with a larger N1 amplitude in the tapping positive compared to the tapping negative conditions. There was no significant effect of Condition (i.e., listening vs. tapping) [$F(1,14) = .77$, $p = .40$].

Figure 3 about here

In the second shaded box around 300 ms after the stimulus onset in Figure 3 (262-364 ms), which was within the N2 window, there was a significant Condition*ShiftDirection interaction [$F(1,14) = 15.06$, $p < .001$] at 316 ms. Pairwise comparisons showed a significantly larger N2 in the tapping positive condition than in the tapping negative condition [$p < .01$]. In contrast, no significant difference was observed between the listening negative and the tapping negative conditions. N2 amplitudes in the listening positive condition were not significantly different compared to the tapping positive condition. Additionally, no significant difference was observed between the listening negative and the listening positive conditions. A main effect of ShiftDirection [$F(1,14) = 32.44$, $p < .001$] indicated a larger N2 amplitude in the tapping positive condition compared with the tapping negative condition. There was no significant effect of Condition [$F(1,14) = .19$, $p = .67$].

In order to evaluate the ERN in the negative and the positive shift conditions, we included an epoch (*T-1*) immediately preceding the error epoch (*T0*) in the stimulus-locked ERP analysis of a 2×2 repeated measures ANOVA. It included within-subjects variables of Position (*T-1* vs. *T0*) and ShiftDirection (negative vs. positive) (Figure 4). The shaded boxes represent the significant time windows for ERP magnitude analyses: N1: 62-154 ms and N2: 246-406 ms. At 119 ms (N1), a Position by ShiftDirection interaction was found [$F(1,14) = 31.55$, $p < .001$]. Pairwise comparisons showed a greater N1 amplitude in the tapping positive *T0* compared to the tapping positive *T-1* [$p < .01$]. A greater N1 amplitude was found in the tapping positive *T0* condition compared to the tapping negative *T0* condition [$p < .01$]. In contrast, no significant differences were found between the tapping negative *T-1* and the tapping negative *T0* conditions and between the tapping negative *T-1* and the tapping positive *T-1* conditions. A main effect of ShiftDirection [$F(1,14) = 25.30$, $p < .001$] was observed, with a larger N1 amplitude in the tapping positive condition compared to the tapping negative condition. There was a main effect of Position (*T-1* vs. *T0*) [$F(1,14) = 5.70$, $p < .05$], with a larger N1 at *T0* than at *T-1*.

Figure 4 about here

At 280 ms (within the significance window of 246-406 ms, N2), a Position*ShiftDirection interaction effect was found [$F(1,14) = 25.13$, $p < .001$] (Figure 4). Pairwise comparisons showed that the N2 amplitude for the tapping negative *T0* was lower than the tapping negative *T-1* [$p < .05$]. In contrast, a greater N2 amplitude was found in the tapping positive *T0* compared to the tapping positive *T-1* condition [$p < .01$]. While a significant difference was observed between the tapping negative *T0* and the tapping positive *T0* conditions [$p < .01$], no significant difference was identified between the tapping negative *T-1* and the tapping positive *T-1* conditions. A main effect of ShiftDirection [$F(1,14) = 30.03$, $p < .001$] indicated a larger N2 amplitude in the tapping positive condition than in the tapping negative condition. There was no significant effect of Position (*T-1* vs. *T0*) [*F*(1,14) = .69, *p* = .42].

3.2.2 Response-locked data analyses

We initially compared response-locked ERPs between the negative and the positive shift conditions using a one-way repeated measures ANOVA. Significant differences were found within the time window of 356-410 ms (a figure relating the comparison was not shown, but refer to Figure 5). At 374 ms (rising phase of CNV-like negativity), a larger CNV-like negativity was observed in the tapping negative condition compared with the tapping positive condition [*t*(14) = -5.22, *p* < .001].

Figure 5 about here

We then conducted our second analysis using a 2×2 repeated measures ANOVA with within-subject variables of Position (*T-1* vs. *T0*) and ShiftDirection (negative vs. positive) (Figure 5). No significant 2-way interaction effect was identified. However, at 374 ms, a main effect of ShiftDirection was observed [*F*(1,14) = 6.22, *p* < .05], with a larger CNV-like negativity observed in the tapping negative condition compared with the tapping positive condition. There was no significant effect of Position (*T-1* vs. *T0*) [*F*(1,14) = .60, *p* = .51].

3.3 Correlation between physiological and behavioral data

Figure 6 about here

To evaluate the functional significance of ERP components reported above, we examined correlations between those ERP activities at the time of shifts (*T0*) and subsequent error correction performance at *T+1* (both negative and positive shifts). For each participant, we scored the peak amplitude and the peak latency of N1, N2 and the CNV-like negativity: 1) N1, TN: mean amplitude: 1.61 (SD = .83), mean latency: 140.40 (SD = 26.12), TP: mean amplitude: -.23 (SD = 1.15), mean latency: 105.73 (SD = 23.54); 2) N2, TN: mean amplitude: 1.03 (SD = 1.02), mean latency: 252.0 (SD = 19.38), TP: mean amplitude: -1.82 (SD = .98), mean latency: 328.0 (SD = 29.38); 3) CNV-like negativity, TN: mean amplitude: -.1.02 (SD = .91), mean latency: 484.67 (SD = 44.43), TP: mean amplitude: -1.51 (SD = 1.16), mean latency: 581.20 (SD = 54.69).

We found that the peak latency of the CNV-like negativity was positively correlated with the normalized error correction performance at *T+1* in the tapping negative condition (i.e., the earlier the peak, the better the error correction performance with the negative shifts) [$r(15) = .569$, $p < .05$]. On the other hand, the peak latency of the CNV-like negativity was negatively correlated with the normalized error correction performance at *T+1* in the tapping positive condition at a trend level of significance (i.e., the later the peak, the better the error correction performance with the positive shifts) [$r(15) = -.439$, $p = .10$]. Finally, to investigate the effect of post-error processing which is stimulus locked (N1 and N2), we also scored the peak amplitude and the latency of N1 and N2, including those in the listening conditions. However we did not find significant associations with error correction performance.

4. Discussion

We aimed to investigate whether the ERP components associated with post-error processing (N1 and N2 which could be associated with ERN) or the ERP relating to the expectation of a subsequent stimulus following an error (contingent negative variation - CNV) would be critical to error correction performance. Our stimulus-locked ERP data analysis revealed, 1) increased auditory N1 amplitude for the positive shift condition while decreased auditory N1 modulation for the negative shift condition; and 2) a second enhanced negativity (N2) in the stimulus-locked tapping positive condition, compared with the tapping negative condition. However, they (including N1 and N2 in the listening conditions) were not associated with error correction performance. On the other hand, our response-locked ERPs showed an early latency for our CNV-like negativity in the tapping negative condition, compared with the tapping positive condition, and the earlier the peak, the better the error correction performance in the tapping negative condition. There was a trend that the later peak latency was associated with better error correction performance in the tapping positive condition. Hence, we have found a direct neural mechanism involved in error correction: *response-locked CNV-like negativity*.

The contingent negative variation (CNV) is sensitive to the anticipation of (and attention to) an incoming stimulus in order to prepare a subsequent behavioral response (Tecce, 1971, 1972). As in many previous CNV studies (Cui *et al.*, 2000), it appeared at fronto-central sites (maximally detected at FCz as in the current study). On the other hand, the Bereitschaftspotential (BP or readiness potential) would show a left-lateralized distribution if right-handers perform the task as in our study (Vaughan *et al.*, 1968). As such, the fronto-centrally localized CNV is unlikely to be associated with the BP. A slow build-up of negativity or the ‘type B CNV (Tecce, 1972)’, is observed when participants are certain of the next stimulus’ onset; its peak would be close to the forthcoming stimulus onset (so called, ‘expectancy wave’; Walter *et al.*, 1964). We observed that the CNV-like negativity was more rapidly formed in the tapping negative condition compared with the tapping positive condition. We interpret this as the neural signature of incoming stimulus anticipation (*T+1*), because the brain would need to prepare for the next response earlier after experiencing the unexpectedly early stimulus. On the other hand, this preparation would need to occur relatively later, after experiencing an unexpectedly late stimulus. These opposing neural patterns were directly translated into behavioral performance: the earlier the peak, the better the error correction performance in the tapping negative condition; conversely, the later the peak, the better the error correction performance in the tapping positive condition (at a trend level of significance). Our observation on the CNV-like negativity was consistent with ERP studies examining CNV elicited during time perception tasks. Macar *et al.* (1999) reported that the CNV amplitude reflected the length of temporal estimates, and/or an index of time-based decision making and response (Macar & Vidal, 2009). As such, our results provide evidence that the CNV-like negativity is associated with error correction (correction of response timing) in our sensorimotor paradigm. However, as we had a relatively small sample size, future studies may want to further confirm the role of the CNV-like negativity in error correction by systematically varying stimulus inter-onset interval with a larger sample size.

We have identified the presence of the error correction in our behavioral data, with faster error correction performance observed with the tapping positive condition compared with the tapping negative condition. Our behavioral results are consistent with previous studies (Praamstra *et al.*, 2003; Repp, 2001a; Thaut *et al.*, 1998) including our own (Bijsterbosch *et al.*, 2011a; Bijsterbosch *et al.*, 2011b). Our data suggest that there may be different error correction processes for the correction of negative vs. positive errors. When the positive shift occurred, it provided a ‘time gap’ in which a tap was made, but an associated tone was not heard, thus generating increased selective attention in anticipation of the missing tone. This would result in the positive shifts appearing more ‘distinctive’ to the participants compared to the negative shifts (Itti & Baldi, 2009; Logan & Zbrodoff, 1979). Therefore, the tapping positive condition was more rapidly recognized, permitting for faster error correction. This process though would be more variable, compared with that of the tapping negative condition, as shown in Repp (2002), because negative shifts (those occurring earlier than expected) would have to be corrected reactively. The increased attention owing to the distinctive stimulus is also reflected through the auditory N1 which has been shown to reflect sensory processing associated with selective attention (Hillyard *et al.*, 1973; Näätänen *et al.*, 1978; Picton & Hillyard, 1974). As such, we observed an enhanced negativity at around 100 ms (auditory N1) in the tapping positive condition while the auditory N1 was reduced in the tapping negative condition.

Interestingly, the tapping negative condition manifested markedly suppressed auditory N1 amplitudes compared to the tapping positive condition and was even lower than the passive listening conditions (see Figure 3). The decreased tap-tone asynchrony in the tapping negative condition is insufficient to explain the auditory N1 in terms of reduced selective attention and perception. When a perceptual stimulus was delivered in proximity to the execution of the movement, ERP components, particularly the auditory N1, were suppressed, demonstrating that a temporal contiguity between action and sound was sufficient to trigger such a suppressed auditory N1 response (Hazemann *et al.*, 1975; Horváth, 2013a, 2013b, 2014; Horváth *et al.*, 2012). ‘Action-related auditory suppression’ would explain the suppression of N1 in the tapping negative condition, compared with the listening negative condition (Horváth *et al.*, 2012).

We found an enhanced negativity at around 300 ms (N2) in the tapping positive condition compared to the tapping negative condition. N2 amplitudes in the listening conditions showed a similar pattern as we observed with the N1. Auditory N2 is known to be associated with signaling a mismatch between sensory input and stored memory representations, permitting recognition of novelty (Näätänen & Winkler, 1999). The difference in N2 amplitudes between the tapping positive and the listening positive conditions could be explained by ‘the production effect’ (MacLeod *et al.*, 2010). For example, it has been shown that musical melodies played by the subject with normal auditory feedback are better recognized (which was associated with enhanced N2) compared to melodies that were only heard by the subject and not actively produced by them (Brown & Palmer, 2012; Mathias *et al.*, 2015). Thus, this enhanced N2 will in turn lead to stronger memory retention. With better memory representation of the stimuli, the memory violation had alerted the participants of the mismatch to a greater degree (associated with positive shifts), which was translated into the enhanced auditory N2 modulation. Indeed, Mathias *et al.* (2015) reported the supplementary motor and premotor areas associated with auditory N2. Our finding of increased N2 in fronto-central areas in the tapping positive condition (see Figure 3, N2 topographic map for tapping positive condition) is consistent with the report of Mathias *et al.* (2015). Likewise, the increase in the auditory N2 could be associated with the mismatch negativity (MMN; Näätänen *et al.*, 1978). The MMN is a negative component that arises when an irregularity is introduced in a structured auditory sequence (Näätänen, 1992), with its largest amplitude observed typically over the fronto-central areas (for a review, see Näätänen *et al.*, 2007). Alternatively, our finding of increased N2 could be related to the feedback-related negativity (FRN). The FRN is a negative deflection that is recorded with a peak latency of around 250 ms, elicited following an unexpected negative feedback (i.e., to an inaccurate response) (Miltner *et al.*, 1997). Our SMS tasks were not designed to offer a feedback stimulus itself, however, it is possible that the shifted stimulus at *T0* functions as a feedback signal due to its dissimilarity with the preceding tones (*T-4* to *T-1*). An enlarged FRN visible in the tapping positive *T0* around 300 ms could therefore be the reflection of such an unexpected negative feedback.

Praamstra *et al.* (2003) hypothesized that ERN was involved in the phase shift paradigm, because participants would perceive the time-shifted sequence as an error. While they found the presence of the ERN only in the positive shift condition (but not in the negative shift condition), they suggested that the ERN might be related to the N2 component, due to its similar scalp distribution and latency to N2. However, their ERN analysis was conducted by comparing the ERP waveform at *T0* with pooled ERP data comprised with *T-3*, *T-2*, and *T-1*. One way to test this suggestion was to compare the ERP waveforms at *T0* directly to *T-1*, which maintains the same signal to noise ratio between the conditions. Our results demonstrated that the response-locked ERP waveforms showed no significant differences across the tapping conditions at *T0* and *T-1*, showing no sign of ERN (Figure 5). Furthermore, our stimulus-locked data analyses showed the tapping negative *T0* with more reduced ERP responses compared with *T-1*. In addition, ERP waveforms with lower amplitudes were observed in the tapping negative condition compared with the listening conditions (Figure 3). If ERN was related to the error correction in the SMS tasks, higher N2 amplitude would be present in the tapping negative condition, compared with the listening negative condition. We can therefore conclude that the N2 modulation had little association with the ERN.

There are some issues to consider in interpreting the results of this study. First, we found the association between the CNV-like negativity and the behavioral data. However, no statistical correction procedures to adjust for possible type 1 errors were included in analyzing the associations between the ERP components and the error correction behavioral variables. Hence, the results must be interpreted with caution. However, our two opposite direction of associations (a: the earlier the CNV, the better the error correction in the tapping negative condition, b: a trend level of relationship between the later CNV and better error correction in the tapping positive condition) show that the 'chance finding' is less likely. Given that these associations are consistent with the studies indicating the CNV as an index of the internal temporal estimates, we suggest that such CNV-like negativity may have the same role in the current SMS paradigm. Second, our participants had a high rate of missing taps (approximately 15% of total tones). Consequently, we have relatively small number of trials in the tapping conditions compared to the listening conditions. This would possibly be due to a relatively long EEG data acquisition time (approximately 1 hour). Nonetheless, the average trials for the response-locked analysis remained adequate in both conditions (over 100 trials). Third, participants performed the task with their eyes closed, which was ensured by the experimenter next to them. This procedure was to avoid frontally-generated artifacts associated with eye movements. It is well known that the alpha activity in EEG increases with eyes-closed particularly across the occipital cortex (Klimesch *et al.*, 2007). However, because we measured ERPs at a fronto-central site (FCz), the potentially enhanced alpha-band activity would have minimal effect on our results. Supporting this, ERP components (both amplitude and latency) were not different between eyes-open and eyes-closed conditions in an auditory discrimination task (Polich, 1986). The eyes-closed procedure has frequently been employed in other finger tapping studies (Knyazeva *et al.*, 1997; Sammler *et al.*, 2007) because it minimizes focal changes associated with visual input (e.g., participants were prone to observe their finger movements) which could be incorrectly associated with the processing of auditory stimuli (Barry *et al.*, 2007). Furthermore, because the potential alpha activity would always be present across our experimental conditions, it would be canceled out in our condition-wise comparisons. Finally, no strict attention control was implemented in the listening condition. Asking to report the number of the irregularities in each block would have been an option but such measures were not implemented in Praamstra *et al.* (2003). We were concerned with the possibility of producing an additional effect from 'counting', which might have been pronounced in the listening condition.

5. Conclusions

In conclusion, we investigated whether the neural components associated with post-error processing (N1 and N2) or the component relating to the expectation of a subsequent stimulus following an error (CNV) would be critical to error correction performance. We have found evidence that the CNV-like negativity is associated with error correction during the SMS task. We therefore conclude that expectation of sensory stimuli (associated with CNV) may be intimately related to error correction. ERP components associated with post-error processing (N1 and N2) were differentially associated with tapping negative and positive conditions, such that the positive shifts were associated with higher amplitude. Nonetheless, their impact on error correction could be indirect. Our study provides the basis from which further research on the role of the CNV in perceptual and motor timing can be developed.

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