

Medial frontal negativities predict performance improvements during motor sequence but not motor adaptation learning

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Abstract

Alterations in our environment require us to learn or alter motor skills to remain efficient. Also, damage or injury may require the relearning of motor skills. Two types have been identified: movement adaptation and motor sequence learning. [Doyon et al. \(2003, Distinct contribution of the cortico-striatal and cortico-cerebellar systems to motor skill learning. *Neuropsychologia*, 41\(3\), 252-262\)](#) proposed a model to explain the neural mechanisms related to adaptation (cortico-cerebellar) and motor sequence learning (cortico-striatum) tasks. We hypothesized that medial frontal negativities (MFNs), event-related electrocortical responses including the error-related negativity (ERN) and correct-response-related negativity (CRN), would be trait biomarkers for skill in motor sequence learning due to their relationship with striatal neural generators in a network involving the anterior cingulate and possibly the supplementary motor area. We examined 36 participants' improvement in a motor adaptation and a motor sequence learning task and measured MFNs elicited in a separate Spatial Stroop (conflict) task. We found both ERN and CRN strongly predicted performance improvement in the sequential motor task but not in the adaptation task, supporting this aspect of the Doyon model. Interestingly, the CRN accounted for additional unique variance over the variance shared with the ERN suggesting an expansion of the model.

KEYWORDS

correct-response-related negativity, cortico-striatal system, medial frontal negativity, motor learning, performance monitoring

1 | INTRODUCTION

Behavior is a dynamic process. The environment is constantly prompting us to alter our behaviors and learn new motor patterns in order to achieve our goals and even to survive. Two of the main forms of such motor learning are those requiring new movement sequences and those requiring motor adaptation. For example, each time one

purchases a new car and the steering reacts differently, one must adapt a well-known motor sequence in order to operate the vehicle safely. This contrasts with the learning of new behavioral sequences, such as when a pianist learns a new sequence of notes by repeating them, often thinking of them as a “chunk” of finger movements. These two types of motor skill can be observed in various other types of physical movements, including more dynamic sports skills

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(Masaki & Sommer, 2012). Traditional studies of motor learning have not examined this differentiation. Instead, in the field of sport psychology, relatively dynamic movements are used as tasks to test theories of motor skill acquisition (e.g., the Bachman ladder climb task, ball throwing, and balance task; Bachman, 1961; Wulf et al., 2001), whereas neuroscience research has used more adaptation learning tasks with lesser movements (e.g., joystick-use, lever pressing) to prevent contamination of muscular artifacts due to body movements. Thus, studies on motor learning have not adequately compared the neural bases of the differences in the sequence and adaptation task types. Recent studies with patients have provided evidence that the basal ganglia (BG) is linked to motor sequence learning, whereas the cerebellum is linked to motor adaptation (Doyon & Benali, 2005; Meissner et al., 2018; Panouillères et al., 2015).

Doyon and colleagues have proposed a model to capture neural mechanism differences underlying adaptation versus motor sequence learning, where motor adaptation is the capacity to compensate for environmental changes, and motor sequence learning is the acquisition of new motor patterns (Doyon & Benali, 2005; Doyon et al., 2003). In their model, motor sequence learning is predominantly associated with the cortico-striatal system, whereas motor adaptation primarily relies on the cortico-cerebellar system. When motor adaptation is fully learned and has become autonomous (Fitts & Posner, 1967), performing the acquired skill activates the cerebellum, parietal cortex and motor-related cortical region, but not the striatum. In contrast, during motor sequence learning, the striatum, the parietal, and motor-related structures, but not the cerebellum, are involved in execution of the acquired skill. Their model has been empirically supported by an fMRI study that examined brain activity of expert knitters while learning a new stitching pattern versus adaptation to operating a joystick to reach a target (Doyon & Benali, 2005). Thus, the cortico-striatal system and the cortico-cerebellar system appear to serve distinct functions in terms of practicing or learning a motor skill, although an interaction between the systems may occur during the early stages of motor learning.

In order to test this model, we employed a strategy involving performance monitoring, which is conceptualized as a process that increases when we start performing an unwanted response (Ullsperger & Von Cramon, 2001) or when the response requires increased control (Nieuwenhuis et al., 2003; van Noordt et al., 2015; van Noordt & Segalowitz, 2012). For example, when we detect an ongoing erroneous response, we normally attempt to correct it quickly in order to respond correctly, ideally before the error is completed. After we have committed an error, we typically prepare more cautiously for the next opportunity in order to reduce the probability of another erroneous response. This often results in increased response times compared to responses that follow correct responses, referred to as post-error slowing (PES) (Gehring

& Knight, 2000; Klein et al., 2007), although some studies have questioned the functional significance of PES as performance monitoring (Fu et al., 2019; Gehring & Fencsik, 2001; Gehring & Knight, 2000; Hajcak et al., 2003; Mathalon et al., 2002; Nieuwenhuis et al., 2001) and even ascribed PES to an orienting response effect due to shorter intertrial intervals (Van der Borghet et al., 2016).

Additionally, in relation to motor learning, performance monitoring is a primary mechanism to acquire a novel skill. Motor learning theories have traditionally relied on two memory systems, recall memory and recognition memory (Adams, 1971; Schmidt, 1975). According to the closed-loop theory (Adams, 1971), the memory trace is used to initiate a movement by recalling previously experienced actions, whereas the perceptual trace works as an internal model that is compared with intrinsic feedback about ongoing movements, detecting discrepancy between the internal model and the feedback (i.e., error detection). Thus, strengthening the perceptual trace is fundamental to motor learning, leading to the development of error-detection capabilities (e.g., Schmidt & White, 1972). Thus, the degree of capability to detect and correct movement errors can determine the level of mastery of the motor learning (Sherwood, 1996).

With this perspective, performance monitoring is a mechanism that underlies our ability to modify actions based on performance outcome that is provided by both internal and external feedback (Masaki et al., 2015). This behavior modification is, of course, regarded as learning, and numerous studies have investigated performance monitoring in the context of reinforcement learning (Holroyd et al., 2004). Similarly, an increase in response control is called for when a prepotent response needs to be changed or inhibited. In both cases, cortical activation yields an electroencephalogram (EEG) response resulting in a frontocentral negative-going component at the scalp (Falkenstein et al., 1991; Gehring et al., 1993). In the field of cognitive neuroscience, several interpretations have been given to this electrophysiological response associated with performance monitoring, including error detection, conflict detection, inhibition of erroneous response, and subsequent error correction (Ullsperger & Von Cramon, 2001).

Numerous studies of performance monitoring have suggested that this frontocentral negativity is generated from medial prefrontal regions, especially the anterior cingulate cortex (ACC) (e.g., Holroyd et al., 1998; van Noordt et al., 2016). It should be also noted that some studies have suggested a possibility that the frontocentral negativity elicited by erroneous responses, referred to as the error-related negativity (ERN), may be initiated by an earlier network response in the supplementary motor area (SMA) (Bonini et al., 2014; Emeric et al., 2008; Fu et al., 2019). In the current study, we make use of this performance monitoring response in the context of error commission that yields the ERN (or Ne), a member of the family of medial frontal negativities (MFNs).

Performance monitoring also occurs, of course, during the production of correct responses as this is how incipient error commission is detected. Given that the errors committed in these tasks are normally slips or impulsive responses rather than genuine errors of judgment, it may mean that this MFN is a sign of improved attention control, which would be consistent with evidence from multiple sources. For example, the degree of positive versus negative polarity on a correct trial relates to the likelihood of committing an error on the next trial; a greater positivity seems to reflect a relative lack of monitoring or a transient deficit of attention control, leading to an increased likelihood of making an error. Correct trials preceding errors show lesser medial frontal negativity (i.e., greater positivity referred to as error-preceding positivity: EPP, Ridderinkhof et al., 2003) than do correct trials preceding other correct trials (see also, Allain et al., 2004; Hajcak et al., 2005; Masaki et al., 2012). Similarly, increasing the vigilance required by the task increases the amplitude of the MFN (Pailing & Seglowitz, 2004) and across individuals, those with attention deficits produce smaller MFNs (Groen et al., 2008; Liotti et al., 2005) while hypervigilant individuals exhibit larger MFNs (Gehring et al., 2000). More recently, in a series of experiments decomposing the EEG signal into latent components, the medial prefrontal cortex portion of the MFN was shown to increase in amplitude when situations demanded increased vigilance in general and not for monitoring errors nor feedback per se (van Noordt et al., 2015, 2016, 2017).

Thus, both correct and error trials may yield an EEG indication of the degree of effortful vigilance shown by the participant on the task. This association of MFN with increased performance fits with other paradigms yielding midfrontal negativities, such as the Contingent Negative Variation in continuous anticipation of an upcoming stimulus (Brunia & van Boxtel, 2001) and in learning paradigms including those with nonhuman primates (Stamm, 1984).

Because motor learning relies heavily on attention control (Kaiser et al., 2015; Rosch et al., 2013; Toplak & Tannock, 2005), it is reasonable to presume that the trait that the MFN reflects (as opposed to the current state) may account for some variance in the attention control that is required for acquisition of a novel motor skill. For the current study, we make use of the MFN as a general neural correlate of attention control in the service of performance as an underlying mechanism of performance monitoring, whether elicited during incorrect or correct responses.

1.1 | MFN and performance monitoring

Event-related potentials (ERPs) associated with performance monitoring have been examined in tasks involving motor adaptation (Anguera et al., 2009), motor sequence learning (van

der Helden et al., 2010), and serial reaction times (SRTT, Beaulieu et al., 2014; Rüsseler et al., 2003). However, only two studies among these examined changes in ERN as a function of motor learning and these showed a discrepancy in their findings: Beaulieu et al. (2014) found a positive correlation ($r = .49$) between performance improvement and increase in ERN amplitude (i.e., changes from early blocks to late blocks in a selective response time task), whereas Rüsseler et al. (2003) failed to find any significant correlation.

As Holroyd and Coles (2002) outline in their model, the MFN results from a BG/ACC system involved in performance monitoring, where the BG modifies dopaminergic activities by influencing the pathway ascending to the ACC before it generates the ERN (Holroyd & Coles, 2002; Schultz et al., 1997). More recently, research involving diseases of the BG reported a reduction in amplitude of the ERN, supporting a link between the two (for Parkinson's patients: Falkenstein et al., 2001; Seer et al., 2017; and for Huntington's patients: Beste et al., 2006).

Together with the motor learning studies involving the ERN, the Holroyd and Coles (2002) model suggests that the scalp-recorded MFN is an indirect marker for BG activity during performance monitoring in motor learning tasks. As mentioned above, of particular interest here is the demonstration that the degree of MFN even during correct responses (i.e., correct-response-related negativity: CRN; Mathalon et al., 2002) is a marker for performance monitoring in that its amplitude predicts accuracy on the subsequent trial (Ridderinkhof et al., 2003). The tight integration of performance monitoring and attention control in the BG/ACC network is central to the current study. We hypothesize that individual differences in the ERN and CRN reflecting the degree of performance monitoring should correlate with performance improvements of a novel motor skill. However, we hypothesize that this correlation should appear only when the BG are involved in motor learning, that is, during the motor sequence task (MST) that relies more on the BG, but not in a motor adaptation task that relies more on the cerebellum. For the current study, we elicit the ERN and CRN in a spatial conflict task separate from the motor learning tasks.

Some studies have suggested that the factor of intrinsic versus extrinsic motivation affects the amplitudes of MFNs (Boksem et al., 2006), and so we have included this manipulation in our paradigm by having the MFNs elicited in two conditions, one with a monetary reward/punishment and one without (Hajcak et al., 2005). These motivation-driven effects have been often interpreted from perspectives of reinforcement learning theories that rely on a function of the basal ganglia as being involved in the reward system. Consistent with this, fMRI studies that manipulated monetary reward also found better performance in a motor learning task with increased activities of the striatum (e.g., Widmer et al., 2016). Not surprisingly, both monetary

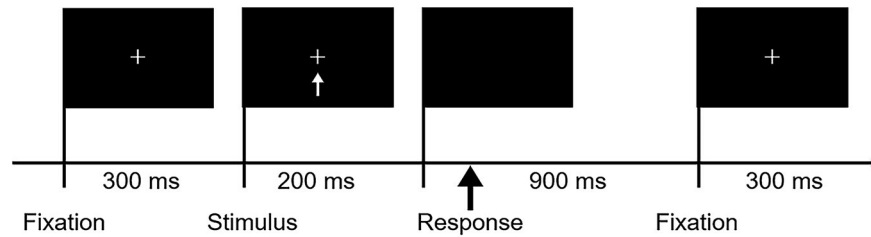


FIGURE 1 Procedure of the Spatial Stroop task used in the present study. Participants were asked to respond to the pointing direction of the white arrow stimulus (i.e., up or down), but not to the arrow location. We referred to our task as a Spatial Stroop task based on Kornblum's model (1992) that can classify all types of SRC tasks in terms of overlap among relevant property of stimulus, irrelevant property of stimulus, and response dimension. According to his model, our task is classified as Type 8 that is same as classical Stroop task

reward and punishment are also associated with behavioral improvement (i.e., learning) (Abe et al., 2011) including performance on both motor sequence and adaptation tasks (Galea et al., 2015; Steel et al., 2016) of the sort used in the current study. As well, individual differences in sensitivity to monetary reward and punishment affect motor control (Robinson & Bresin, 2015). Thus, without being able to specify the specific cognitive functions underlying the relation, motivation is often seen as a moderating variable in tasks such as those used here.

It should be noted that correct responses may include initial covert erroneous movements that also elicit the ERN on behaviorally correct trials. Such correct-response trials during response-conflict tasks are more likely to engender simultaneous double responses (incorrect and then correct) during incongruent stimulus presentations, producing peripheral muscular activity referred to as “the partial error” that occurs preceding the corrective peripheral muscular activity (Masaki et al., 2012). Previous studies clearly showed ERNs elicited by partial errors that manifest in the electromyogram (EMG) (Masaki & Segalowitz, 2004). Therefore, recording peripheral muscle activity can let us separate the MFNs on correct-response trials into those associated with covert erroneous responses (partial-error ERN) and pure-correct responses (pure CRN). Given that the CRN can be classified as an MFN, the CRN elicited by pure-correct responses should also predict performance improvements in a motor sequence learning task, but not in a motor adaptation task.

In this study, we examined performance improvement in a motor sequence learning task and a motor adaptation task, based on the model of Doyon and colleagues. We expected that participants would adequately acquire those relatively simple motor skills, and thus, their performance would reach asymptote with practice in a single session. Thus, given our position that the cortico-striatal system is more involved in motor sequence learning, whereas the cortico-cerebellar system is more involved in motor adaptation, we hypothesized that the amplitudes of the MFNs, including the ERN, the partial-error ERN, and the CRN, should predict improvement of motor sequence skill but not improvement of motor adaptation skill.

2 | METHOD

2.1 | Participants

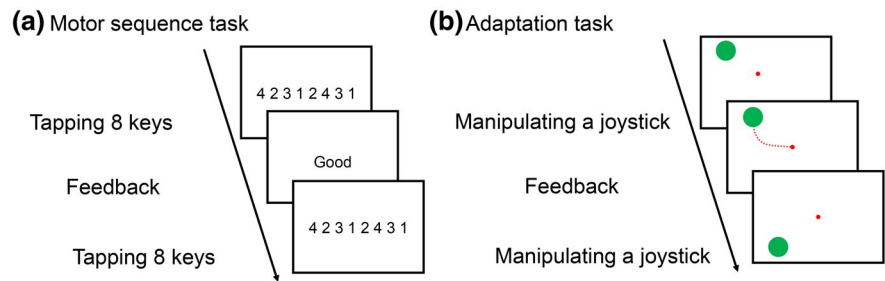
Forty-four participants (16 men, 28 women, mean age \pm SD = 21.6 ± 2.3 years) were recruited from Waseda University's Faculty of Sport Sciences. We excluded six participants from the ERN analysis because of their small number of overt errors (fewer than six errors, Olvet & Hajcak, 2009) and two participants who declined to attend the motor learning session (Day 2). Consequently, 36 participants (13 men, 23 women) were used for correlation analyses between ERPs and performance in the motor learning tasks. Thirty-five were right-handed (mean handedness scores = +89.4) and one was left-handed (handedness score = -80.0) (Edinburgh Handedness Inventory, Oldfield, 1971). Participants had normal or corrected-to-normal vision and were paid 3,200 yen (about 30 U.S. dollars) for their participation. Written informed consent was obtained. This study was approved by the Waseda University Ethics Committee. We recorded EEGs during the execution of a Spatial Stroop task in the first session and tested two motor learning tasks in the second session (on a different day).

2.2 | MFNs recording session

A spatial conflict task (hereafter referred to as the “Spatial Stroop task”; Masaki, et al., 2012) was performed while EEG was recorded (see Section 2.4 below for more details) in order to record ERN and CRN amplitudes associated with motivational processing (Figure 1). This task can be classified as the same type (Type 8 ensemble) as the standard Stroop task according to a taxonomy of stimulus-response compatibility paradigm proposed by Kornblum (1992), conceptually overlapping in properties among relevant stimulus, irrelevant stimulus, and response. For the standard Stroop task, dimensions of the relevant stimulus (color), irrelevant stimulus (color word), and response (color naming) all overlap in terms of color. For our task, they all overlapped in terms of spatial properties.

Each trial began with a white fixation cross ($1.1^\circ \times 1.1^\circ$) on a black background that was presented at the center of a

FIGURE 2 Procedures for the motor sequence (1a, left) and adaptation tasks (1b, right)



cathode ray tube (CRT), placed 1 m in front of the participant. The fixation was followed by a white arrow (either pointing up or down) that was presented above or below the fixation for 200 ms with an eccentricity of 0.6° visual angle (between centers of fixation and arrow). The task was to respond to the direction of the arrow but not to the location (i.e., above or below fixation), by briskly lifting their middle finger when the stimulus appeared. Participants were also encouraged to respond within 600 ms following the stimulus onset. When response time exceeded 600 ms, the message “too late” was presented as a visual feedback in the center of the CRT for 500 ms.

During the experiment, the participants rested both forearms and palms comfortably on a flat board to minimize any movements other than middle finger responses. They were instructed to place their middle fingers on microswitch keys, mounted on the board oriented along the midplane in front of the participant. The weight of the finger while relaxed was enough to depress the key during the foreperiods. A plastic plate ($30 \times 20 \times 1$ mm) was attached on the end of the key. The displacement of the key by lifting the middle finger led to switch closure and the overt response onset could be identified. Both speed and accuracy were emphasized. Congruent and incongruent stimuli were randomly presented with 50% probability. Hand placement was counter-balanced across further and nearer keys.

We tested two conditions, a motivation condition and a non-motivation condition. In each condition, participants performed four blocks (72 trials/block). In the motivation condition, a correct response was monetarily rewarded (+10 yen: about +10 cents), whereas an error response was monetarily penalized (−10 yen). After every block finished, participants were informed of the cumulative total amount of acquired money in that block. In the non-motivation condition, neither monetary reward nor punishment was contingent upon a response. The order of condition was counter-balanced across participants using either an ABAB or BABA sequence; the condition was changed every two blocks.

2.3 | Motor learning tasks

At least 1 day after the EEG recording with the Spatial Stroop task, participants performed in a second session both the motor sequence task and the adaptation task. Each task

was composed of 16 trials \times 10 blocks. Both movement time and correct response rate were measured in each task. In the motor learning session, stimuli of both tasks were presented in the center of a liquid crystal display monitor, placed 70 cm in front of the participant. The order of the two motor learning tasks was counter-balanced across participants.

2.3.1 | The motor sequence task

The task was to press keys in a predetermined sequential order as quickly and accurately as possible. Each trial began with a fixation (2,000 ms duration) that was replaced by an array of digits representing the predetermined sequence as an imperative stimulus (Figure 2a). Participants were asked to press keys “V,” “B,” “N,” and “M” of a computer keyboard (corresponding to the key code 1, 2, 3, and 4, respectively) when the imperative stimulus appeared. The predetermined sequence order to be executed was the fixed order $4 \rightarrow 2 \rightarrow 3 \rightarrow 1 \rightarrow 2 \rightarrow 4 \rightarrow 3 \rightarrow 1$. Participants performed the task with the four fingers of their dominant hand. After an execution of each trial, visual feedback (i.e., either “correct” or “error” written in kanji characters) was presented for 1,000 ms. Prior to the experiment, the participants practiced button presses in a simple sequence order (i.e., $1 \rightarrow 2 \rightarrow 3 \rightarrow 4 \rightarrow 1 \rightarrow 2 \rightarrow 3 \rightarrow 4$) for one block (16 trials) to become familiar with the button locations. The task was programmed using a stimulus-presentation software (Presentation, Neurobehavioral Systems, Inc).

We note that our task was not an SRTT task but a motor learning task that has been used in cognitive neuroscience studies (e.g., Kami et al., 1995). In the motor sequence task, RTs to individual stimuli in a fixed sequence were not measured because participants repeatedly performed the fixed sequence, and a novel sequence was not inserted in secret to evaluate the occurrence of implicit learning unlike the SRTT. In the motor sequence task, in which the learner explicitly strives to shorten the total movement time, improvements in movement time were of interest.

2.3.2 | The adaptation task

The task was to move a cursor (i.e., a circle, 0.3 cm in diameter, visual angle 0.2°) from the starting position to a target

circle (1.6 cm in diameter, visual angle 1.5°) as quickly and accurately as possible, using a joystick with the dominant hand. Adaptation was required because the moving cursor was programmed to displace 30° counter-clockwise. Each trial began with the presentation of a target in one of eight possible positions on the circumference of an imaginary circle and the fixed starting position in the center of this circle (Figure 2b). The participant started operating the joystick when the target appeared. The moving speed of the cursor was determined by the participant's operation of the joystick. After execution of a trial, visual feedback about the trajectory of the moving cursor was presented for 1,000 ms (Figure 1b). The trajectory of the moving cursor was sampled at 17 Hz. The next trial started 10 ms after the feedback ended. Before the experiment, participants practiced the task without the displacement for one block (16 trials) to become familiar with the operation of the joystick device. Movement time was measured as the duration between the starting time when the cursor moved five pixels from the starting position (i.e., 25 mm on the monitor) and the moment the cursor touched the contour of the target circle. Trials on which the participant failed to touch the target circle were classified as incorrect trials. The task was programmed using a java-based stimulus-presentation software (Processing, <https://processing.org/>, ver2.2.1, Inc).

2.4 | EEG recordings

During the Spatial Stroop task, the EEG was recorded from 128 sites with Ag/AgCl electrodes. Horizontal electrooculograms (hEOG) were recorded from the left and right outer canthi, and vertical electrooculograms (vEOG) from above and below the left eye. These were recorded with a bandwidth of DC to 205 Hz, using a BioSemi Active Two system (BioSemi Inc.). The system uses “offset” units consisting of CMS (common mode sense) and DRL (driven right leg) electrodes that were kept below 20 through the experiment to assure high quality data. Off-line the EEG was re-referenced to the average reference, and band-pass filtered from 0.1 to 30 Hz (24 dB) when ERPs were analyzed with Brain Vision Analyzer 2 (BVA2, Brain Products). Bipolar electromyograms (EMG) were recorded from the extensor digitorum muscle in the left and right forearms with Ag/AgCl electrodes using the BioSemi Active Two system and were off-line high-pass filtered with 5.31 Hz and full-wave rectified with the BVA2. EMG was collected in order to identify covert movements whether of the correct hand or the incorrect hand. All physiological signals were digitized at a rate of 1,024 Hz.

2.5 | ERPs

Processing of EEG and EMG data was performed with the BVA2. We obtained ERPs time-locked to both the EMG

onset and the response onset (i.e., switch closure). We averaged ERPs separately for pure-correct trials that did not contain any erroneous muscular activities, partial-error trials (as identified via EMG responses), and overt error trials. Only incompatible trials were analyzed for the ERN. Partial errors were characterized by rectified EMG activity of the incorrect arm that did not lead to a switch closure, which was then followed by corrective EMG activity within 250 ms. We excluded from ERP averaging those trials in which response time exceeded 600 ms, was less than 100 ms, or vertical or horizontal EOG voltages exceeded a threshold of $100 \mu\text{V}$ during the analysis epoch, ranging from -600 ms to $+600$ ms relative to the response (or EMG) onset. Ocular movement artifacts included in EEGs were corrected before averaging, using the algorithm developed by Gratton et al. (1983) that Brain Vision Analyzer provides for users.

To determine the onset of the EMG, that is, the EMG response time (EMG-RT), we used the criterion of a deflection of 4.0 standard deviations of the rectified EMG compared to a baseline of -100 to 0 ms pre-stimulus using a semiautomatic macro procedure implemented in Brain Vision Analyzer. For each trial, the onset of the EMG response was determined by moving backward in time from where the upward slope of the rectified EMG waveform crossed the criterion until the amplitude ceased decreasing (Masaki et al., 2000; Smid et al., 1992). The validity of the EMG onset detection was also visually inspected on each trial, and any invalid EMG onset was corrected manually. Because the extension of the middle fingers is suitable to record clear EMG for anatomical reasons, we could clearly detect even small EMG activities as a partial error.

Both the ERN and CRN were quantified as mean voltages in the period from 0 to 100 ms following the error and correct responses, respectively, at FCz, the site at which both components were maximal in the overall average. A pre-response baseline was calculated as mean voltage ranging from -500 to -400 ms as this captures the immediate pre-stimulus onset period for most trials and avoids incorporating the positivity before the response into the baseline. For amplitudes of the response-locked ERPs (ERN and CRN), we conducted a two-way ANOVA with repeated measures on response type (correct/error) and condition (motivation/non-motivation). For the EMG-locked ERPs, we conducted a two-way ANOVA with repeated measures on response type (pure correct/partial error/overt error) and condition (motivation/non-motivation).

2.6 | Correlation analyses

We examined individual differences in improvement of behavior and performance monitoring. Then, we calculated improvement in accuracy in the motor learning tasks, by subtracting Block 2 from Block 1 and Block 10 from Block 2. Improvement of accuracy on the motor learning

tasks was correlated with improvement time in both tasks, response-locked ERN, EMG-locked ERN (overt error), partial-error ERN, response-locked CRN (including partial error), EMG-locked CRN (pure correct), response-locked CRN (including partial error), and EMG-locked CRN (pure correct) in each condition. We also report corrected correlations in each motor learning task with a false discovery rate (FDR) adjustment in two ways, based on each task separately ($N = 20$) and based on the tasks together ($N = 40$), from combinations of MFN measures (response-locked ERN and CRN, and EMG-locked (partial error) ERNs and CRN, 5) * condition (motivation/non-motivation, 2) * block comparisons (2) for each task.

3 | RESULTS

3.1 | Spatial Stroop task

3.1.1 | Behavioral responses

Figure 3 shows mean response time (left panel) and error rate (right panel) in the Spatial Stroop task. For response time, a two-way ANOVA revealed longer response times on incongruent trials than on congruent trials ($F(1, 35) = 394.76, p < .001, \eta_p^2 = 0.92$). Neither a motivation condition effect ($F(1, 35) = 1.15, p = .29, \eta_p^2 = 0.03$) nor an interaction of motivation by congruency was obtained ($F(1, 35) = 0.18, p = .67, \eta_p^2 = 0.01$). For error rate, a two-way ANOVA revealed both main effects of stimulus congruency ($F(1, 35) = 107.92, p < .001, \eta_p^2 = 0.76$) and motivation condition ($F(1, 35) = 10.51, p = .003, \eta_p^2 = 0.23$). An interaction of stimulus type by condition was also significant ($F(1, 35) = 10.47, p = .003, \eta_p^2 = 0.23$). A simple effect analysis revealed that error rate on incompatible trials was lower in the motivation condition than in the non-motivation condition (16.9% vs. 21.3%, $t(35) = 3.44, p = .002, d = 0.44$). Three quarters of the participants produced at least 15 errors, with the other nine ranging from 6 to 14. In order to see whether the correlational results described below were dependent on those with fewer errors, we repeated the analyses with only those with 15 or more errors. The correlation results were the same. We note that others have suggested that as few as six error trials are needed for highly reliable ERN

waveforms (Olivet & Hajcak, 2009). In addition, mean number of “too late” trials (RT > 600 ms) with *SEM* was 0.53 ± 0.17 on congruent and 1.67 ± 0.30 on incongruent in the motivation condition and 0.58 ± 0.13 on congruent and 2.36 ± 0.40 on incongruent trials in the non-motivation condition, respectively. A two-way ANOVA revealed no difference in too-late errors in the non-motivation condition compared with the motivation condition ($F(1, 35) = 2.56, p = .12, \eta_p^2 = 0.07$) but more too-late errors on incongruent trials than on congruent trials ($F(1, 35) = 29.23, p < .001, \eta_p^2 = 0.46$). No interaction was found ($F(1, 35) = 2.65, p = .11, \eta_p^2 = 0.07$).

3.1.2 | EMG-RT

We calculated EMG-RTs on incompatible trials. In the motivation condition, mean EMG-RTs for pure corrects, partial errors, and overt errors were 290 ms (*SEM*: 6.3), 218 ms (4.9), and 223 ms (6.2), respectively. In the non-motivation condition, mean EMG-RTs for pure corrects, partial errors, and overt errors were 284 ms (6.0), 213 ms (4.3), and 220 ms (6.0), respectively. A two-way ANOVA revealed main effects of response type ($F(2, 70) = 359.60, p < .001, \eta_p^2 = .91$) and condition ($F(1, 35) = 5.95, p = .020, \eta_p^2 = 0.14$). EMG-RT for pure corrects was longer than for both partial errors ($t(35) = 23.22, p < .001, d = 2.24$) and overt errors ($t(35) = 20.91, p < .001, d = 1.83$). RT did not differ between partial errors and overt errors ($t(35) = 2.42, p = .063$). No interaction was found ($F(2, 70) = 0.36, \varepsilon = 0.87, p = .66, \eta_p^2 = 0.01$).

3.1.3 | MFNs

Figure 4 shows grand-averaged waveforms of the response-locked ERPs (left panel) and the EMG-locked ERPs (right panel). The response-locked MFNs were greater on trials with errors compared to correct responses. A two-way ANOVA revealed a significant main effect of response type ($F(1, 35) = 138.96, p < .001, \eta_p^2 = 0.80$) but not condition ($F(1, 35) = 0.15, p = .70, \eta_p^2 = 0.01$). The interaction was not significant ($F(1, 35) = 1.11, p = .30, \eta_p^2 = 0.03$).

For EMG-locked MFNs, a two-way ANOVA revealed a significant main effect of response type ($F(2, 70) = 49.47, p < .001$,

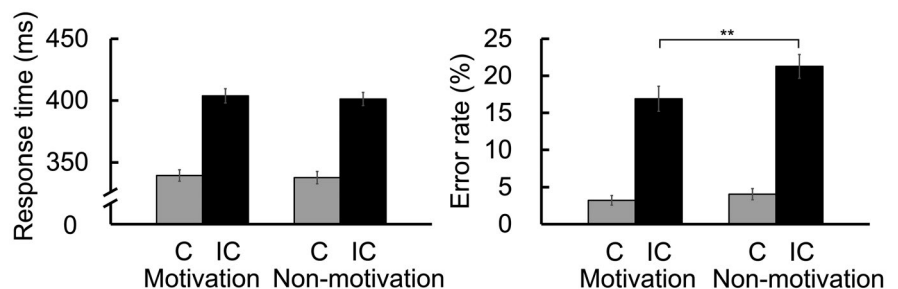


FIGURE 3 Mean response time (left) and error rate (right) for the Spatial Stroop Task

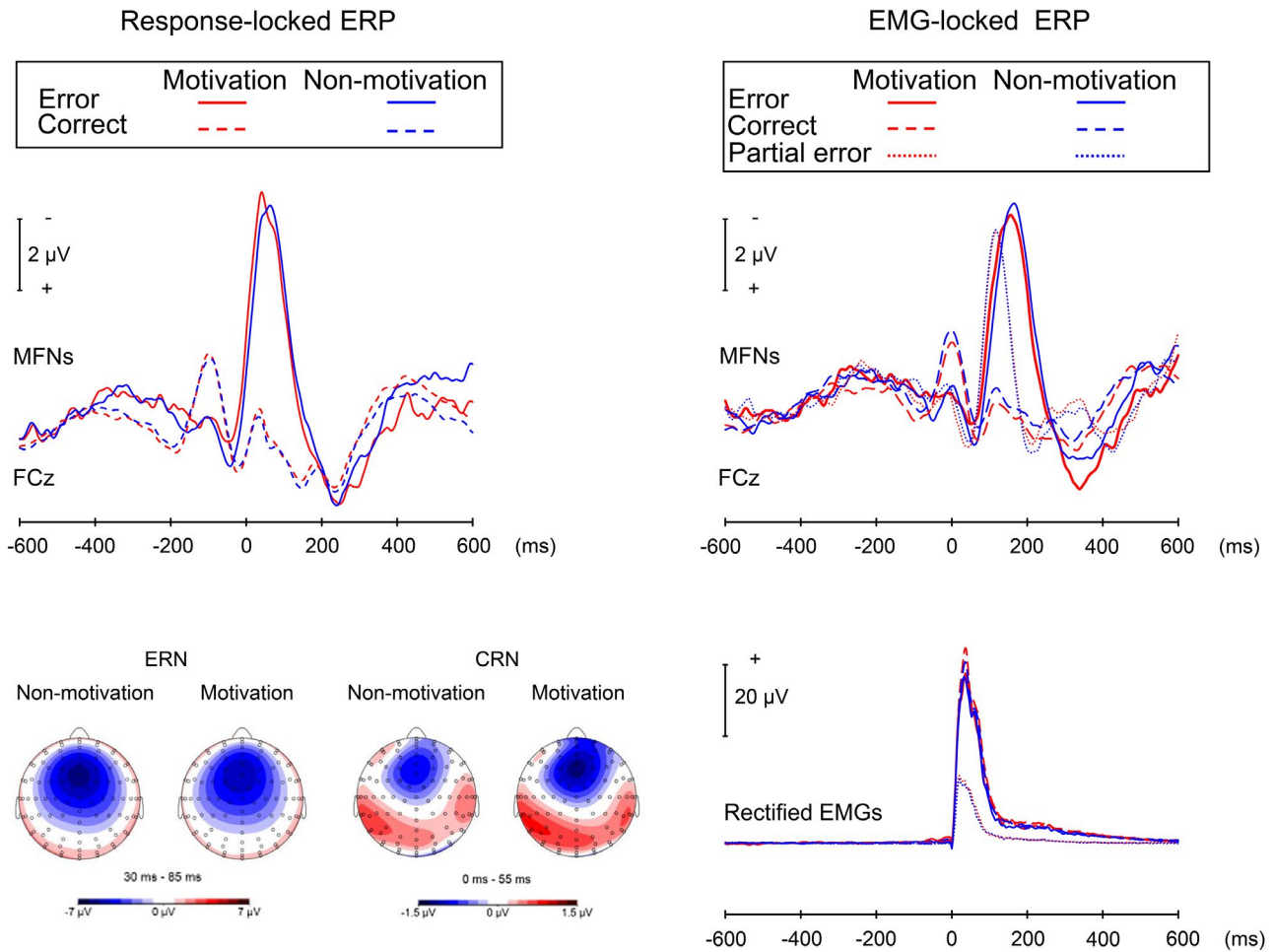


FIGURE 4 Grand-average waveforms at FCz for response-locked (lower left) and EMG-locked (lower right) analyses as well as topographical maps (upper left) and rectified EMG (upper right). In order to illustrate the topographies, we adopted a baseline (−30 to −10 ms before the response onset) and drew the maps based on the peak negativities (time window 0 to 55 ms for the CRN and 30 to 85 ms for the ERN)

$\eta_p^2 = 0.59$), showing that the EMG-locked ERN was greater than the partial-error ERN ($p = .006$) and that the partial-error ERN was greater than the CRN ($p < .001$). Neither main effect of condition ($F(1, 35) = 0.10, p = .75, \eta_p^2 = 0.01$) nor interaction ($F(2, 70) = 0.33, p = .72, \eta_p^2 = 0.01$) was found.

3.2 | Motor learning tasks

3.2.1 | Motor sequence task

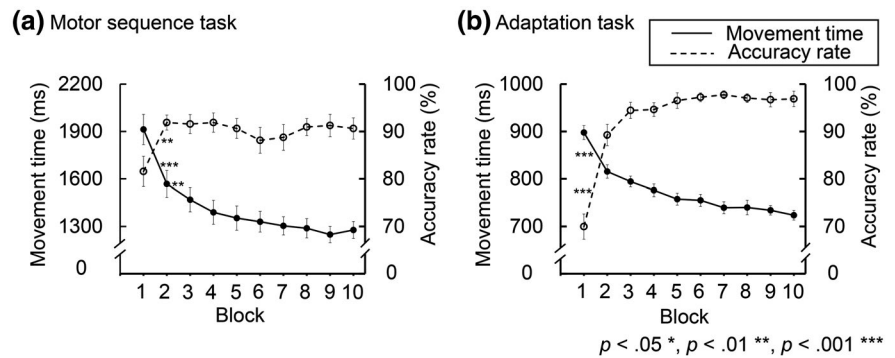
Figure 5a shows mean movement time and accuracy rate in the motor sequence task. A one-way ANOVA revealed improvements in movement time as a function of practice ($F(9, 315) = 72.85, \epsilon = 0.35, p < .001, \eta_p^2 = 0.68$). The movement time became significantly shorter with practice during earlier stages (Block 1 vs. Block 2, $t(35) = 11.13, p < .001, d = 0.82$; Block 2 vs. Block 3, $t(35) = 4.80, p < .001, d = 0.29$). There were no other significant differences between adjacent blocks ($ps > .10$). The improvement in movement time from

Block 2 to Block 10 was significant, $t(35) = 9.28, p < .001, d = 0.82$. A main effect of block was also significant for accuracy ($F(9, 315) = 3.31, \epsilon = 0.56, p = .007, \eta_p^2 = 0.08$), higher in Block 2 than Block 1 ($t(35) = 4.12, p < .001, d = 0.73$). There were no other significant differences between adjacent blocks ($ps > .10$), nor from Block 2 to Block 10, $t(35) = 0.91, p = .37, d = 0.20$.

3.2.2 | Adaption task

Figure 5b shows movement time and accuracy rate in adaption task. A one-way ANOVA revealed improvements in movement time ($F(9, 351) = 46.61, \epsilon = 0.51, p < .001, \eta_p^2 = 0.57$), with significantly reduced times from Block 1 to Block 2 ($t(35) = 9.47, p < .001, d = 0.95$). There were no other significant differences between adjacent blocks ($ps > .10$). Movement time decreased from Block 2 to Block 10 ($t(35) = 7.02, p < .001, d = 1.24$). A main effect of block was also significant for correctness ($F(9, 315) = 45.03, \epsilon$

FIGURE 5 Movement time and accuracy rates across blocks for the motor sequence and adaptation tasks



= 0.42, $p < .001$, $\eta_p^2 = 0.56$), with higher correct rate in Block 2 than in Block 1 ($t(35) = 8.05$, $p < .001$, $d = 1.30$). There were no other significant differences between adjacent blocks ($ps > .10$), but there was an improvement in accuracy from Block 2 to Block 10, $t(35) = 3.75$, $p < .001$, $d = 0.65$.

3.3 | Correlation analyses

3.3.1 | Motor sequence task

On the motor sequence task, there were significant negative correlations (ranging from -0.33 to -0.69) between ERP amplitudes and improved movement time from Block 2 to Block 10 (Table 1), indicating that the larger the improvement, the more negative the MFN amplitude. In addition, these negative correlations were found for all MFNs, including the response- and EMG-locked ERNs and the response- and EMG-locked CRNs. However, no significant correlations were observed between MFN amplitude and improvement over the earliest stages (i.e., from Block 1 to Block 2). The relations between B2-to-B10 improvement in movement time and the MFNs are illustrated in Figure 6. Adjusting for the number of correlations ($N = 20$) performed using FDR did not alter the pattern of significances.¹

We also wanted to see whether the number of errors on the Spatial Stroop task yielding the MFNs influenced the ERP amplitudes such that the correlations between ERN or CRN amplitudes and motor sequence improvement could be a function of general performance skill. To examine this, we entered the number of errors on the first

step of the regression predicting movement time improvement, followed by the response-locked ERN and the response-locked CRN amplitudes in subsequent steps. Doing so did not alter the pattern of significant effects shown in Table 1, and hardly altered the correlations at all. Also, there were no significant semi-partial correlations between movement time improvement and the number of errors in either the motivation ($p = .80$) or the non-motivation ($p = .77$) conditions. Thus, the number of errors did not significantly influence these relationships.

3.3.2 | Adaptation task

The performance improvements in the adaptation task showed a dramatically different pattern of correlations with the ERP amplitudes compared to that of the motor sequence task (Table 1). Only two were significant, and these involved the performance improvement in the initial phase (Block 1–Block 2) with only the partial-error ERNs in the two conditions ($r = -.42$, $p = .01$ in the motivation condition; $r = -.41$, $p = .013$ in the non-motivation condition). All other correlations were not significant. Once again, adjusting for the error rate did not alter the pattern of results. Adjusting for the number of correlations performed within the task ($N = 20$) did not alter this pattern of significances, but with the more stringent FDR adjustment ($N = 40$), the two significant effects disappeared.¹

3.3.3 | Comparison of MFN correlations with the two tasks

To compare the strength of the correlations between the MFN and each of the two tasks, we applied a multiple regression analysis to the response-locked ERN amplitudes in the motivation condition, including performance improvements of the motor sequence task and the adaptation task as independent variables. This produced a significant multiple determination coefficient ($R^2 = .27$, $p = .006$; adjusted $R^2 = .22$, $p = .006$). The standard partial regression coefficients for the movement

¹The a priori hypotheses addressed correlations between the ERP amplitudes as measured several ways and performance improvement on the two tasks. Not surprisingly, the various ERP amplitudes correlate well across participants thereby indicating that we do not have 20 independent correlation values, making the FDR test conservative. However, for both tasks, FDR adjustments did not alter the pattern of significant effects. In fact, pooling the number of analyses from both tasks for an FDR based on 40 correlations also did not alter the pattern for the motor sequence task.

	Motor sequence		Adaptation	
	B1–B2	B2–B10	B1–B2	B2–B10
<i>Motivation conditions</i>				
Response-locked ERN (overt error)	–0.05	<u>–0.51</u> **	–0.33	0.16
Response-locked CRN (including partial errors)	0.17	<u>–0.66</u> ***	–0.25	0.01
EMG-locked ERN (overt error)	–0.07	<u>–0.43</u> **	–0.27	0.17
EMG-locked CRN (pure correct)	0.01	<u>–0.67</u> ***	–0.25	–0.01
Partial-error ERN	0.01	<u>–0.51</u> **	<u>–0.42</u> *	–0.01
<i>Non-motivation conditions</i>				
Response-locked ERN (overt error)	0.06	<u>–0.43</u> **	–0.29	0.23
Response-locked CRN (including partial errors)	0.13	<u>–0.65</u> ***	–0.24	0.05
EMG-locked ERN (overt error)	0.02	<u>–0.44</u> **	–0.32	0.20
EMG-locked CRN (pure correct)	0.02	<u>–0.66</u> ***	–0.26	–0.01
Partial-error ERN	–0.13	<u>–0.47</u> *	<u>–0.41</u> *	0.13

Note: Bolded r values in the table indicate remaining significance after false discovery rate (FDR) correction with 20. Underlined r values in the table indicate remaining significance after FDR correction with 40.

* $p < .05$; ** $p \leq .01$; *** $p \leq .001$.

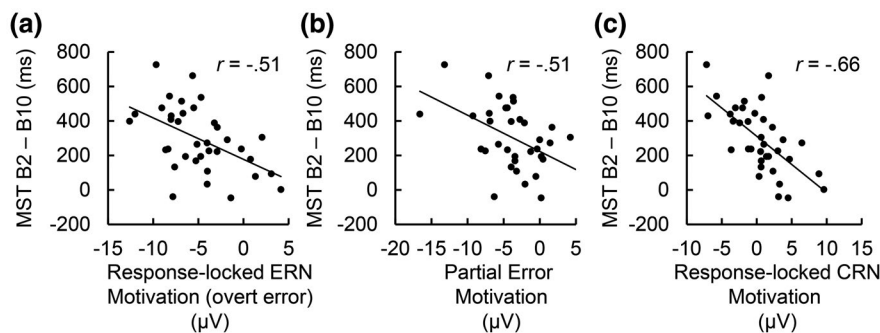


FIGURE 6 Scatterplots of performance improvement (Blocks 2 through 10) and selected ERN and CRN amplitudes

sequence task was significant ($\beta = -.49$, $p = .002$), but not for the adaptation task ($\beta = .10$, $p = .52$). A similar pattern emerged for the CRN, where only the movement sequence task showed unique variance ($\beta = -.66$, $p < .001$) and not the adaptation task ($\beta = -.07$, $p = .607$). The same pattern was obtained for the other MFN correlations with the two tasks, with all MFN correlations with the movement sequence task improvement showing significant unique variance (all p 's ranging from <0.001 to 0.01) and none with the adaptation task improvement being statistically significant (all p 's $> .25$).

3.3.4 | Correlations among the CRN, ERN, and motor sequence task

Unexpectedly, we noticed that the correlations for the CRNs were considerably greater than for the ERNs. Not

surprisingly, the CRNs and ERNs correlated highly with each other, with values ranging between $r = .49$ and $.76$ (all p 's $< .002$). Regression analyses were computed and partial correlations were used to determine the unique variance explained by each in terms of improvement in movement time from B2 to B10 in the motor sequence task. Across all conditions the CRN accounted for significant unique variance (p 's $< .003$) but the ERN did not (p 's $> .42$; see Table 2). Once again, adjusting for the error rate did not alter the pattern of unique variances, that is, solely due to CRN sources.

4 | DISCUSSION

We tested whether trait MFNs can predict performance improvement during motor skill acquisition in a motor sequence task and a motor adaptation task. Importantly, improvement

TABLE 2 Zero-order and semi-partial correlations between movement time improvement in the motor learning task from Block 2 to Block 10 and ERN and CRN amplitudes from regression analyses in motivation and non-motivation conditions. Note that in all cases, the CRN variance absorbs that of the ERN and contributes unique variance itself

	Correlations	
	Zero-order	Semi-partial
<i>Motivation conditions</i>		
Response-locked ERN (overt error)	-0.51*	-0.07
Response-locked CRN (including partial errors)	-0.66**	-0.42*
EMG-locked ERN (overt error)	-0.43*	0.09
EMG-locked CRN (pure correct)	-0.67**	-0.52**
Partial-error ERN	-0.51*	-0.02
EMG-locked CRN (pure correct)	-0.67**	-0.43*
<i>Non-motivation conditions</i>		
Response-locked ERN (overt error)	-0.43*	-0.04
Response-locked CRN (including partial errors)	-0.65**	-0.50**
EMG-locked ERN (overt error)	-0.44*	-0.10
EMG-locked CRN (pure correct)	-0.66**	-0.50**
Partial-error ERN	-0.47*	-0.11
EMG-locked CRN (pure correct)	-0.66**	-0.47**

* $p < .05$; ** $p \leq .01$; *** $p \leq .001$.

patterns over time of both movement time and accuracy were almost identical on the two tasks, allowing a direct comparison in terms of performance improvement. Given that these MFNs associated with performance monitoring are likely influenced by the basal ganglia (Holroyd & Coles, 2002), we hypothesized that their amplitude should predict learning performance in the motor sequence task according to the model of Doyon and colleagues in which the cortico-striatal system is more involved in motor sequence learning and not in the motor adaptation task because of its association with the cortico-cerebellar system (Doyon et al., 2003). Our results were consistent with this hypothesis. Individuals who exhibited larger trait MFN amplitudes showed better performance improvement only in the motor sequence task. This suggests that motor learning tasks should be differentiated at least into those focusing on sequence learning and those involving motor adaptation, as our data show that the neural basis for them differs. This is not generally done in research on motor learning, and therefore, potentially eliminates effects due to confounding differences in task requirements with error variance.

Interestingly, the amplitude of the CRN predicted performance improvement better than did the ERN despite the emphasis in the literature on the ERN. Regression analyses indicated that the CRN could even predict significant

amounts of unique variance (above that accounted for by the ERN) in the movement time of the motor sequence learning task in both the motivation and non-motivation conditions. The ERN did not demonstrate unique variance above that of the CRN. Thus, it appears that the CRN is a superior marker of task improvement. Given this, it may be important to consider what we know about the sources for the two similar but not identical ERP components.

Previous studies have suggested that the ERN is influenced by activities of the basal ganglia. Compared to healthy controls, Parkinson's patients have reduced amplitude of their ERN (Falkenstein et al., 2001; Seer et al., 2017) as do those with Huntington's disease (Beste et al., 2006). The reduction of the ERN for these patients would be expected because these diseases result from the deficiency of dopamine or γ -aminobutyric acid (GABA) in the basal ganglia (Bird & Iversen, 1974; Perry et al., 1973). However, previous studies did not find any significant reduction of the CRN for these patients (with the exception of Seer et al., 2017). Ullsperger and von Cramon (2006) also found that lesions of the basal ganglia reduced the amplitude of the ERN, but not the CRN.

This does not necessarily mean that the ERN and CRN have completely different functional significance, but rather suggests that the basal ganglia might be involved more in error processing than in correct-response processing, and that the negativity resulting on correct trials does not have the same source exactly as the error trials. The ERN and CRN do, after all, intercorrelate highly and previous studies have suggested that the ERN and CRN share similar characteristics (Vidal et al., 2003) or a common psychological foundation (Bartholow et al., 2005). In addition, it has been suggested that both the ERN and CRN might emanate from the ACC (Holroyd & Coles, 2002), indicating the commonality of these components. The common proximal source in the ACC may be a clue to the basis for our results.

Before we consider this, we must acknowledge at least two possible explanations for our findings of the higher correlations for the CRN. The CRN may simply be a cleaner or more stable measure because it is based on a larger number of trials leading to higher signal-to-noise ratio than the ERN, resulting in more stable waveforms. If the number of trials contributing to the ERP is an important factor, then, the response-based CRNs should predict the performance improvement better than the EMG-based CRNs because the associated mean (minimum) number of trials for the motivation and non-motivation conditions were 118.5 (72) and 113.7 (67) and 82.9 (31) and 77.8 (39), respectively. However, the correlations with the B2–B10 improvement on the sequence task ranged only from 0.654 to 0.668. The trivial difference between these values is clearly not related to the number of trials in such a way as to account for the correlational results. Also, the number of trials used that was reported above (minimum of 31, with all means over 75) is more than sufficient to

produce a stable CRN. Similarly, the variation in the number of trials contributing to the various ERN measures did not map onto the correlations with performance improvement. Furthermore, none of the values for the number of trials correlated reliably with the improvement measure (ranging from -0.049 to $+0.093$, all n.s.). Thus, we have no reason to expect that the number of trials per se is an artifact accounting for the significant unique variance in the CRN.

A more interesting second possibility is that the ERN reflects more sources of variance than does the CRN, and the additional sources of variance do not correlate as well with the degree of motor sequence learning. For example, it may be that the CRN reflects the allocation of effortful attention that would be associated with the frontal cortex and ACC. This is compatible with the findings of those who have demonstrated that it predicts the likelihood of making an error on the next trial, where a larger CRN is associated with a reduced chance of making an error (Ridderinkhof et al., 2003). When the individual starts responding in an automatic way leading to a prepotent response, the size of the CRN decreases and the chances of making an error increase. This variation, as a trait, would be reflected as well in the ERN. This effortful attention being marked by activation within the frontal cortex has been long documented in entirely different paradigms (Ford et al., 1994; Stamm et al., 1987).

On the contrary, the ERN reflects not only this trait level of attention allocation, but also an increase when a special warning has been received, such as when the person realizes they are about to press the wrong response key. This is supported by a recent series of papers illustrating how simply warning the person that a more difficult trial block is coming up generates a MFN despite there being no error or response inhibition demand at that time (van Noordt et al., 2015, 2016, 2017). Furthermore, this MFN associated with the warning captures the variance produced in the ERN and the Nogo N2, demonstrating that it may be that the MFN associated with these paradigms is largely a result of sudden increases in allocated attention.

Given this possibility, we would conclude that the ERN reflects the allocation of ongoing attention plus this more acute increase in attention due to the alerting response. This would result in the pattern of correlations found in our study if this second more acute attention increase is not correlated with learning on the motor sequence task. The extra source of variance simply becomes added noise that reduces the correlation, compared to the correlations associated with the CRN. Thus, despite the very high intercorrelation between the ERN and CRN, they differ in their relation to the learning measures.

4.1 | Other considerations

One may raise a question of whether the MFN amplitudes correlated selectively with the improvement of motor sequence task but not the adaptation task due to the task properties of

the Spatial Stroop task being similar to those of the motor sequence task but different from those of the adaptation task. However, the properties of the Spatial Stroop task and the motor sequence task were dissimilar except for using finger movement (one lifting, the other pressing). The Spatial Stroop task requires more cognitive processes (due to the S-R incompatibility inducing response conflict), including stimulus evaluation, response inhibition, and response selection, whereas the motor sequence task requires more motor programming, including motor chunking, smooth finger movements with the predetermined order, and dexterity, according to the memorized motor sequence (more like learning a sequence in piano playing than tapping in response to a signal). The cognitive processes and movement adaptation required for the adaptation task were, if anything, more similar to those of the Spatial Stroop task than were those of the motor sequence task, given that the adaptation task involved compensating for a mismatch between standard hand-eye coordination with the 30° offset. Therefore, it is difficult to explain the current results from the perspective of task similarity.

Another issue for interpretation of the results concerns the generator of the MFN. Some studies have suggested that the SMA may contribute more to the ERN than the ACC (Bonini et al., 2014; Emeric et al., 2008, 2010; Fu et al., 2019). Because the SMA was activated earlier than the ACC when erroneous responses occurred, a recent single-unit recording study concluded that the SMA is responsible for error monitoring (Fu et al., 2019). Of course, receiving the information earlier does not mean that the specific scalp EEG event that we are measuring reflecting an outcome of error monitoring emanates from that source. However, in any case, the SMA has been shown to receive more projections from the basal ganglia than the cerebellum, whereas M1 receives more projections from the cerebellum than the basal ganglia (Sakai et al., 2002; Schell & Strick, 1984). Previous studies have reported that the functional significance of the SMA-basal ganglia circuit is involved in not only cognitive processes, including error monitoring and conflict monitoring (Iannaccone et al., 2015), response inhibition (Watanabe et al., 2015), decision-making (Forstmann et al., 2008), but also motor control (Grafton et al., 1995) and motor sequencing (Fernández-Seara et al., 2009). Thus, regardless of whether the generators of the MFN are primarily in the SMA or ACC, our findings support our interpretation that the MFN reflects some important aspect of motor learning. With respect to the cerebellum, it may be that some other aspect of motor sequencing is influenced by activity from this region, given cerebellar involvement in some aspects of online movement monitoring (Van Broekhoven et al., 2009) and performance monitoring (Peterburs & Desmond, 2016; Peterburs et al., 2012, 2015). However, there is no evidence, we know of that the cerebellum affects scalp-recorded MFNs in healthy subjects.

4.2 | Implications

Our results clearly showed that the MFNs can predict the improvement speed of motor skill acquisition, which can be interpreted as reflecting a general attention skill. Recording the MFNs may provide us with an individual metric for the focusing aspect of what is required for sequence learning. Our next step would be to determine whether training that is known to increase sequence learning skill also increases the size of the CRN and ERN. Similarly, a training program that increases the frontal attention system capacity may increase the amplitude of the CRN and ERN, and if so, our findings would suggest that training would also improve motor sequence learning skill. This has been demonstrated once with mindfulness training. Mindfulness training is reputed to improve attention control (Fissler et al., 2017), and has also been shown to increase the amplitude of the ERN (Smart & Segalowitz, 2017).

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AUTHOR CONTRIBUTION

Takuto Matsuhashi: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Software; Validation; Visualization; Writing-original draft; Writing-review & editing. **Sidney Segalowitz:** Conceptualization; Data curation; Formal analysis; Supervision; Validation; Writing-original draft; Writing-review & editing. **Timothy I Murphy:** Formal analysis; Methodology; Supervision; Validation; Writing-original draft; Writing-review & editing. **Yuichiro Nagano:** Methodology; Resources; Software; Writing-review & editing. **Takahiro Hirao:** Software; Validation; Visualization; Writing-review & editing. **Hiroaki Masaki:** Conceptualization; Data curation; Formal analysis; Funding acquisition; Methodology; Project administration; Resources; Supervision; Validation; Visualization; Writing-original draft; Writing-review & editing.

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