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Revisiting deterministic motor sequence learning: EEG correlates and methodological challenges

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ABSTRACT

Motor sequence learning refers to the transformation of discrete movements into integrated and automatized action patterns, underlying skill acquisition. Electroencephalography (EEG), with its high temporal resolution, enables the investigation of the neural dynamics underlying this process. However, despite a growing number of studies, findings remain fragmented and a framework of EEG correlates of deterministic motor sequence learning is still lacking. In this review, we critically examined twenty-three studies to characterize the EEG correlates associated with deterministic motor sequence learning. We aimed to disentangle sequence-specific neural changes from general practice effects, independently of participants' awareness of embedded regularities. We discuss key methodological aspects, including experimental design, control conditions, and awareness assessment. Despite substantial methodological heterogeneity and weaknesses in experimental control, electrophysiological findings converge on the view that learning reflects a shift toward more efficient processing. Learning-related changes include modulation of midline frontal negativities linked to performance monitoring, reductions in midline theta activity indicative of decreased top-down control demands, alpha-band alterations that may support improved stimulus prediction and motor preparation and beta activity, showing mixed general and sequence effects, supports response-related motor and cognitive plan shifts. Evidence on connectivity is more limited but points to reduced functional coupling during learning, while resting-state theta power and motor beta connectivity appear to predict training-related gains. By synthesizing current evidence, this review provides a critical appraisal of the field and recommendations for future research. contributing to a more consistent and interpretable framework for studying the neurophysiological basis of motor sequence learning.

1. Introduction

In everyday life, it is common to acquire a new skill or adapt a consolidated skill to novel situations. The former occurs, for example, when we learn how to ride a bike or execute a tennis serve, while the latter happens when we ride our bike on an unfamiliar terrain or when we have a brand-new tennis racket with different physical properties. Motor learning may involve the concatenation of movements into a new motor scheme, or the adjustment of a familiar motor scheme to a new environment, requiring the modulation of movements to ensure correct and efficient performance.

From a technical perspective, motor learning can be considered a set of processes associated with practice or experience leading to relatively permanent changes in the capability to respond (Schmidt, 1988). Over the last decades, research has primarily focused on two distinct types of learning: motor sequence learning and sensorimotor adaptation. *Motor sequence learning* refers to the integration of a series of single movements into a coordinated and fluid action scheme that, through repetition and consolidation, enables the acquisition of new skills and the performance of many activities of daily living (e.g., learning to ride a bike) (Doyon et al., 2003; Meissner et al., 2018; Seidler, 2010). *Sensorimotor adaptation* is the ability to flexibly adjust movements in response to changes in the body or the environment (Doyon et al., 2009, 2003) (e.g., riding a bike on a muddy road).

Motor learning has been characterized as a multistage process, including acquisition, followed by a consolidation period and long-term retention (Luft and Buitrago, 2005; Byczynski et al., 2025). A key distinction is between online and offline learning (Dayan and Cohen,

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2011). Online learning refers to performance changes that occur during practice (Kantak and Winstein, 2012), typically within-session improvements, reflecting the acquisition of a new movement pattern or the updating of an existing one. However, learning continues beyond the end of practice, with offline processes supporting stabilization, improvement and consolidation (Dayan and Cohen, 2011; Brooks et al., 2026). These offline enhancements can occur over minutes to hours, or across days (Robertson et al., 2004). Both online and offline processes contribute to long-term retention (Romano et al., 2010).

Extensive research carried out using positron emission tomography (PET) and magnetic resonance imaging (MRI) has identified brain regions and networks involved in both motor learning processes at different learning stages. MRI studies have shown the involvement of numerous cortical and subcortical areas, including primary motor cortex (M1), dorsal premotor cortex, supplementary motor cortex, primary somatosensory cortex, superior parietal lobule, thalamus, putamen, and cerebellum (for a review, see Hardwick et al., 2013). Specifically, distinct patterns of cortico-striatal and cortico-cerebellar activity appear to characterize motor sequence learning and sensorimotor adaptation (Doyon et al., 2009, 2003). During the acquisition of a novel motor skill, motor, prefrontal, and parietal areas are actively recruited, together with the cerebellum and the striatum. However the role of primary motor cortex in motor sequence learning is still debated (Berlot et al., 2020). Following consolidation, the neural representation of the motor routine shifts toward cortico-striatal circuitry in motor sequence learning, whereas in motor adaption this shift occurs toward the cortico-cerebellar loop, reflecting a transition from cognitively controlled to more automatized performance (Doyon et al., 2003; 2009). Recent evidence further support his distinction by showing consistent activation of the basal ganglia during sequence-specific learning (Janacsek et al., 2020; Byczynski et al., 2025; Chen et al., 2026) and the engagement of distinct cerebellar regions across the two types of learning (Bernard and Seidler, 2013).

While numerous studies have focused on identifying the brain areas involved in motor learning and how their activation changes with time and practice, the underlying temporal dynamics remain poorly understood. Owing to its high temporal resolution, electroencephalography (EEG) is well suited for investigating temporal neural patterns underlying cognitive processes. EEG is a non-invasive, portable, and cost-effective technique that offers high versatility in both application and analysis. EEG temporal resolution provides a unique window into the rapid neural processes supporting motor sequence learning. Unlike other neuroimaging techniques that primarily characterize slower changes in regional activation, EEG can resolve the temporal evolution of neural activity within individual trials. This enables the dissociation of neural processes associated with motor preparation, movement execution, performance monitoring, and feedback processing, as well as the characterization of transient oscillatory dynamics underlying these functions. Such fine-grained temporal information is particularly relevant for understanding how skill acquisition and automatization reshape the balance between predictive and reactive control mechanisms during sequence performance. In addition, resting-state EEG recorded prior to task performance can be used to examine oscillatory patterns that may predict subsequent behavioral performance (Lum et al., 2023a; Manuel et al., 2018; Mizuguchi et al., 2019). Conversely, EEG data acquired after task completion provide insights into oscillatory activity associated with consolidation processes (Brokaw et al., 2016; Özdenizci et al., 2017) highlighting its value as a versatile tool for investigating all phases of motor learning. While a recent literature review has addressed EEG studies on sensorimotor adaptation (Reuter et al., 2022), a comprehensive review specifically focusing on EEG investigations of motor sequence learning is still lacking. The present paper aims to fill this gap.

Motor sequence learning is typically assessed using tasks that require participants to repeatedly perform discrete movements (e.g., button presses) according to a repeating pattern. This process generally results in faster responses and increased accuracy, when performing a fixed ordinal sequence compared with randomly sequenced movements. Performance improvements are not solely attributable to more efficient motor programming and execution, but also reflect the binding of individual actions into a unified set (Doyon et al., 2018).

The present review aims to synthesize current findings on EEG changes associated with motor sequence learning in healthy individuals. Specifically, it focuses on studies employing deterministic motor sequences and examines how EEG activity changes as participants learn fixed patterns, either with or without explicit awareness. It focuses on how simple discrete movements are concatenated into a coherent and well-defined action scheme. Furthermore, it differentiates performance improvements driven by general practice effects related to stimulus-response integration from those reflecting sequence-specific knowledge of the ordinal structure (Janacsek and Nemeth, 2012; Janacsek et al., 2020; Müssgens and Ullén, 2015). While the former refers to improvements in speed and accuracy resulting from task repetition, irrespective of any underlying regularity, sequence-specific learning reflects knowledge of the repeated sequential structure.

2. Methods

2.1. Information sources and search strategy

This review is designed as a narrative review that incorporates selected methodological elements from the Preferred Reporting Items for Systematic reviews and Meta-Analysis (PRISMA) guidelines (Page et al., 2021). This ensures a transparent and rigorous approach to study identification, selection and reporting while allowing flexibility in the interpretation of the evidence Three scientific databases — PubMed, Web of Science, and Scopus — were searched using the keywords reported in Table 1 in March 2026. The reference lists of the included studies were also examined to ensure that no relevant papers were missed.

2.2. Eligibility criteria

2.2.1. Inclusion criteria

To be eligible, studies had to be peer-reviewed, written in English, and involve healthy human participants aged 18–65 years. They were required to employ EEG to measure brain activity either during the resting-state (before and/or after motor learning) or during the learning task. Additionally, behavioral data on motor performance needed to be reported to monitor learning progress and relate it to physiological measures. Participants were required to learn a novel deterministic motor sequence through multiple repetitions.

Table 1
Search expression used to identify records in PubMed, Web of Science, and Scopus.

Database	Search expression
PubMed	("motor learning" [Title/Abstract] OR "sequence learning"[Title/Abstract] OR "serial reaction time"[Title/Abstract] OR SRT[Title/Abstract] OR "procedural learning"[Title/Abstract]) AND ("EEG"[Title/Abstract] OR "Electroencephalogra*"[Title/Abstract] OR ERP[Title/Abstract] OR "event-related-potential*"[Title/Abstract])
Web of Science	(((TS=("motor learning") OR TS= ("sequence learning") OR TS= ("serial reaction time") OR TS= ("SRT") OR TS= (procedural learning))) AND (TS=(EEG) OR TS= (electronecephal*) OR TS= (ERP) OR TS= (event-related potential*)))
Scopus	(TITLE-ABS-KEY ("motor learning") OR TITLE-ABS-KEY ("sequence learning") OR TITLE-ABS-KEY ("serial reaction time") OR TITLE-ABS-KEY ("SRT") OR TITLE-ABS-KEY ("procedural learning")) AND (TITLE-ABS-KEY ("EEG") OR TITLE-ABS-KEY (electronecephal*) OR TITLE-ABS-KEY ("ERP") OR TITLE-ABS-KEY (event-related AND potential*)) AND (LIMIT-TO (DOCTYPE, "ar"))

2.2.2. Exclusion criteria

Studies involving animals, clinical populations, older adults, or infants were excluded. Furthermore, studies examining the effects of baseline physiological modulation — such as noninvasive brain stimulation, neurofeedback, pharmacological interventions, hypnosis, or sleep manipulation — were not considered. The present review specifically focuses on studies employing deterministic sequences, as defined by Novén and Karabanov (2026), in which each element can be predicted from prior information within the sequence, whether based on the preceding element or on its position in the sequence. Consequently, studies using probabilistic sequences, in which transition between elements occur according to varying probabilities rather than fixed rules, allowing multiple possible successors for a given element, were excluded.

3. Results

A total of 1916 records were identified, of which 981 remained after duplicates were removed. One author (C.G.) performed the selection, first screening by title, then by abstract and finally by full-text. Based on the eligibility criteria, 23 studies were included in this review (see Fig. 1). Supplementary Table 1 provides a summary of each study. The results are organized into two main sections: methodological approaches adopted to investigate motor sequence learning and its neural correlates. The methodological section describes the primary experimental paradigms employed, controls for general practice effects, and assessment of participants' awareness. The section on neural correlates presents relevant EEG findings, categorized according to event-related potentials, brain oscillations, functional connectivity, and resting-state results. All findings that were reported in the included papers were reviewed, including negative findings.

3.1. Methodological approaches to motor sequence learning

3.1.1. Experimental paradigms

3.1.1.1. Serial reaction time task. The main experimental paradigm employed in the reviewed studies was based on the serial reaction time (SRT) task (Nissen and Bullemer, 1987). In its classical version, participants are instructed to respond as quickly as possible to visual stimuli appearing at one of several spatial locations by pressing the corresponding response key (see Fig. 2 A). Unbeknownst to participants, stimuli are often presented according to a sequence embedded within the task. As training progresses, performance typically improves due to both general practice effects and the acquisition of sequence knowledge. Sequence-specific learning is commonly assessed by comparing performance during sequence and random (or pseudorandom) conditions. A typical implementation consists of several sequence blocks followed by a random block, in which the repeating pattern is removed, and a subsequent reintroduction of the sequence. Learning is usually reflected by progressive performance improvements during sequence blocks and by a transient performance deterioration when the sequence is replaced by random stimuli. This comparison allows researchers to distinguish general practice effects, which influence performance regardless of

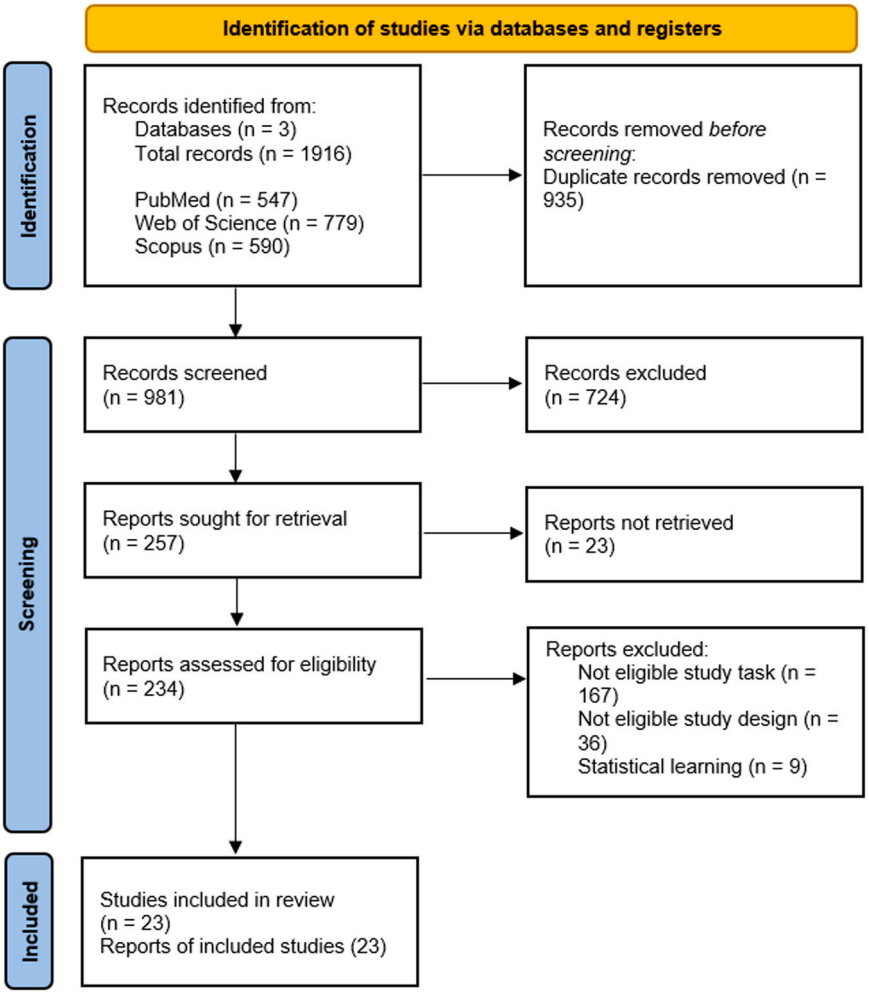


Fig. 1. Review flowchart. PRISMA 2020 flowchart describing the results of the search and selection process.

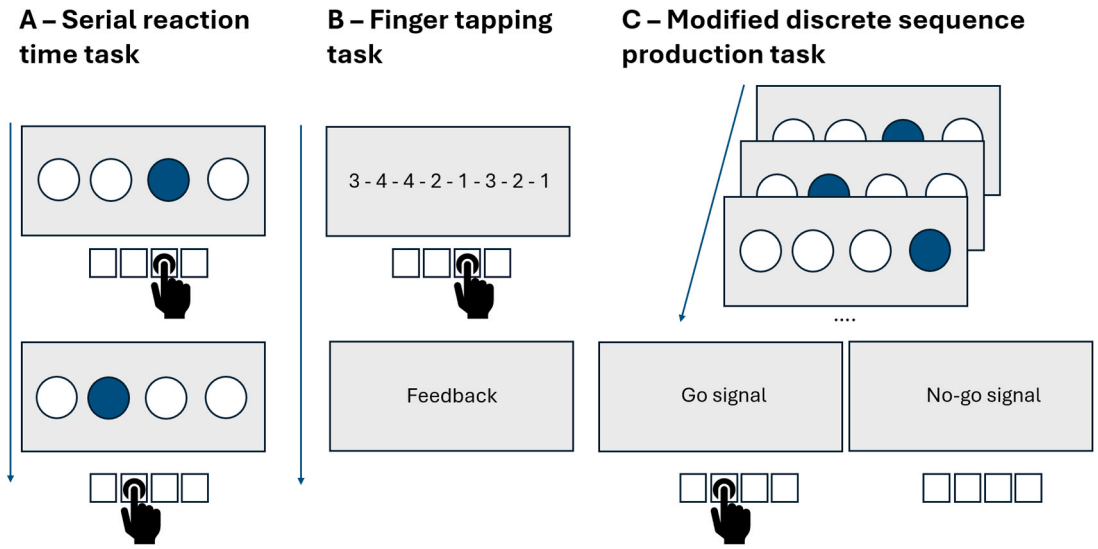


Fig. 2. Representation of the main experimental tasks. *Panel A* illustrates a version of the classical Serial Reaction Time Task (Nissen and Bullemer, 1987), in which a stimulus is presented and participants are required to press the button corresponding to its spatial location as quickly as possible. Individual stimuli are arranged into fixed repeating sequences. *Panel B* illustrates a Finger Tapping Task version, where participants are shown a sequence that must be performed by pressing the corresponding buttons with the aim of reducing execution times. At the end of each trial feedback is presented to assess the performance. Panel C shows a modified version of the Discrete sequence production task (De Kleine and Van Der Lubbe, 2011). Different sequences are presented, followed by a go or no-go signal indicating whether the sequence has to be reproduced manually by pressing the corresponding keys.

sequence structure, from sequence-specific learning reflecting knowledge of the repeated ordinal pattern.

Traditionally, the SRT task measures implicit sequence learning, with participants typically unaware of the deterministic sequence. While most remain unaware, some may acquire explicit knowledge; to identify and exclude these cases, recall and/or recognition tests are generally administered. Variants of the SRT task have also been developed to study explicit learning (Honda, 1998), in which participants are informed about the presence of a repeating sequence.

Among the selected studies, 17 employed the SRT task, mostly using modified versions. In most of the included studies employing the SRT paradigm, participant responded by selecting the response mapped according to the spatial location of the stimulus; four studies (Dyck and Klaes, 2024; Ferdinand et al., 2008; Rüsseler et al., 2003b; Tzvi et al., 2016) focused instead on stimulus identification, where the response was selected according to the stimulus or its features (e.g. color, shape). Most of the considered SRT studies included a random or pseudorandom condition, although the placement of sequence and random blocks varied. In some cases, the random block was placed at the end of the task, or only the final random block was considered when analyzing sequence-specific effects (Beaulieu et al., 2014; Lum et al., 2023a; 2023b; 2019; 2024). Other studies interleaved or placed random blocks among sequence blocks (Farrokhi et al., 2025; Tinga et al., 2020; Tzvi et al., 2016), while some included both sequences and random trials within the same block (Dyck and Klaes, 2024; Ferdinand et al., 2008; Lu et al., 2023; Rüsseler et al., 2003b). The decision to position the control condition has an impact on data analysis and interpretation of results. Placing the random block at the end of the task, after the last fixed sequence block, allows to compare directly sequence-related gains when stimulus-response association is well consolidated. However, it has been pointed out by Fujii et al. (2022), that this design choice could induce arousal variations, due to mental fatigue or sleepiness, that can induce confounding effects on the main outcome. They proposed to embed within the same block sequence and control condition to minimize the arousal effect. Additionally, caution is warranted when evaluating how control conditions are structured, as their degree of homogeneity relative to the fixed sequences and the saliency of specific transitions may confound the interpretation of findings (Pasquali et al., 2019). One study employed sequence blocks with a single random block at the beginning as a baseline (Lawson et al., 2017), a choice made specifically to calculate an individualized threshold aimed at capturing the moment the participant becomes aware of the underlying repeating pattern. In one study (Li et al., 2026) the effect of temporal regularities of fixed or random lengths was investigated, by manipulating response-stimulus intervals. Finally, one study introduced perturbations of the fixed sequence (Chatterjee et al., 2025), assessing general practice effects by disrupting the sequential pattern, resulting in significant behavioral changes once the sequence was learned. Although sequence perturbations are often used to assess sequence-specific learning, they are not equivalent to random blocks. Occasional violations of a learned sequence may induce expectancy violations, conflict monitoring, or strategic slowing, whereas random blocks may additionally require adaptation to a different response structure. Consequently, these control conditions may engage partially distinct processes and should be interpreted with caution.

A few studies employed an explicit variant of the task or included an explicit condition (Dyck and Klaes, 2024; Rüsseler et al., 2003b; Titone et al., 2022).

In most of the reviewed studies, participants performed the tasks using key presses, except for two studies in which participants moved a cursor to reach spatially displaced targets following a predefined pattern (Tinga et al., 2020; Wu et al., 2018), and one study in which participants executed hand movements guided by a humanoid robot (Chatterjee et al., 2025).

Serial reaction time tasks have been employed to assess different stages of learning, including consolidation and retention (Robertson et al., 2004; Pollok et al., 2014; Dyck and Klaes, 2024; Farrokhi et al., 2025). However, some recent accounts have highlighted the lack of long-term changes associated with the classic implicit SRT. For example, Trofimova et al. (2020) reported the classic decrease in reaction times associated with fixed sequences but found no evidence of offline consolidation effects. Accordingly, they suggested that the observed improvement reflected a temporary adaptation to the sequence rather than motor learning. Considering the reviewed literature, two studies employed the SRT to investigate implicit learning across sessions separated by a sleep period. One study, using a modified version of the task, reported offline gains, following a short rest period, only when training was paired with punitive, rather than rewarding feedback, suggesting

that feedback valence may influence offline consolidation processes (Farrokhi et al., 2025). However, this study found no significant effects of overnight sleep on retention, irrespective of the feedback condition. Dyck and Klaes (2024) reported learning-related performance improvements across sessions conducted on different days in a modified version of SRT task, for both implicit and explicit learning, suggesting the presence of long-term retention effects. However, this task differed substantially from both the classical SRT and the version employed by Trofimova et al. (2020), as it included explicit cues signaling transitions between sequence and random trials, which were embedded within the same blocks. Even if not conclusive, these findings provide valuable insights into the effects of long-term retention and offline consolidation in the SRT task. Further studies are needed to investigate the role of the feedback, the nature of the activities performed during the consolidation period, and the influence of task structure on the processes.

3.1.1.2. Finger tapping task. Some studies employed experimental designs in which participants repeatedly practice a sequence of keypresses with the goal of reducing execution time. In general, the sequence is provided from the beginning, so participants are not required to discover it (see Fig. 2B) (Matsuhashi et al., 2021; Mottaz et al., 2024). In these experiments, no random or novel sequences were included, and only motor improvements resulting from sequence practice were measured. Learning is measured as the increased movement time in performing the whole sequence, either by the increased number of buttons presses within a time frame or the overall speed to complete one sequence cycle. A different approach was adopted in a study by Hummel et al. (2003), in which participants first underwent a training session to learn a set of three sequences of increasing complexity, followed by an experimental session in which they performed both the learned sequences and a novel set of sequences matched for difficulty. This design allowed the authors to investigate the effect of sequence complexity while disentangling it from working memory load. Although the study was not specifically designed to assess sequence learning, the comparison between movement sequences of different complexity may provide insights into neural activity associated with the execution and processing of sequential motor actions.

3.1.1.3. Discrete sequence production task. One study employed the discrete sequence production task (Verwey, 2001), a bimanual task in which participants responded to single stimuli by pressing the corresponding keys. Stimuli were arranged into discrete sequences of 6–7 key presses that through repeated practice resulted in improved reaction times and accuracy (Verwey, 2024). Differently from the classic SRT task, the fixed pattern is not embedded into a continuous series of stimuli, but it is presented as a discrete sequence with clear start-stop boundaries. Compared with the finger tapping paradigms described above, participants practice multiple sequences and stimuli are presented one at a time before execution, allowing preparatory processes to be studied more directly. At the end of training, a test phase with a novel, unfamiliar sequence was included as a control condition (Abrahamse et al., 2013). De Kleine and Van Der Lubbe (2011) modified this paradigm by introducing a go/no-go signal following the presentation of several fixed sequences, separated by a preparatory interval (see Fig. 2 C). In the presence of a go signal, participants executed the entire sequence; in the presence of a no-go signal, they inhibited the response. This modification allowed the separate investigation of the execution phase and the preparatory phase of motor sequence learning.

3.1.1.4. Other tasks. In addition to the paradigms outlined above, relatively few alternative task designs have been employed to investigate motor sequence learning. Chatterjee et al. (2025) employed an approach built on the SRT task, by implementing a 3D robot-guided hand movement task. In this paradigm, participants replicated the directional movements of a humanoid robot; the movement pattern was fixed, except for some trials in which the learned sequence was perturbed either spatially or temporally. Other authors (Bellomo et al., 2018) investigated both implicit and explicit motor learning by manipulating participants' awareness through different execution strategies. In their paradigm, participants performed 20 key presses on a small keypad matrix using a single finger, the keys lit up according to distinct patterns. In the explicit condition, the keys lit up in pairs and participants had to follow up by pressing the buttons for 10 cycles. In the implicit condition participants saw one key at a time, requiring them to complete 20 sequential button presses. No random or novel sequences were included in this paradigm. Even if the task is the same between the two groups the longer sequence in the implicit condition lowered the chance for them to develop awareness of the fixed pattern.

3.1.2. General practice effect control

An important methodological consideration in motor sequence learning studies is the inclusion of a control condition to disentangle sequence-specific effects from general practice effects. Table 2 reports whether each reviewed study included such a control. Most reviewed studies, particularly those employing the SRT paradigm, incorporated a control condition in which stimuli were presented in a random or pseudorandom order. Sequence-specific learning is assessed by subtracting the performance between sequence and control condition (Janacsek and Nemeth, 2012; 2013). In motor sequence learning studies involving finger tapping or other explicit tasks, a control condition is still valuable, but sometimes it is not included. Such controls may involve a novel sequence never seen by the participant, an unfamiliar sequence that shares some elements with the learned sequence, or sequences in which a subset of elements has been perturbed. Although such control conditions are useful for isolating sequence-specific effects, novelty or expectation disruption may engage additional cognitive processes that can influence the interpretation of sequence-specific effects.

Table 2
List of included studies specifying whether the experimental task was implicit (Imp), explicit (Exp), or both (Imp and Exp), and indicating the presence of controls for sequence-specific effects and for participants' awareness.

Study	Learning type	Sequence control	Awareness control
Beaulieu, 2014	Imp	Yes	No
Bellomo, 2018	Imp and exp	No	No
Chatterjee, 2025	Imp	Yes	No
De Kleine and Van Der Lubbe, 2011	Exp	Yes	Not applicable
Dyck and Klaes, (2024)	Imp and exp	Yes	Yes
Farrokhi, 2025	Imp	Yes	No
Ferdinand, 2008	Imp and exp	Yes	Yes
Fujii, 2022	Imp	Yes	Yes
Hummel, 2003	Exp	Yes	Not applicable
Lawson, 2017	Imp	Yes	Yes
Li, 2026	Imp	Yes	No
Lu, 2023	Imp and exp	Yes	Yes
Lum, 2019	Imp	Yes	Yes
Lum, 2023a	Imp	Yes	Yes
Lum, 2023b	Imp	Yes	Yes
Lum, 2024	Imp	Yes	Yes
Matsuhashi, 2021	Exp	No	Not applicable
Mottaz, 2024	Exp	No	Not applicable
Rüsseler, 2003b	Imp and exp	Yes	Yes
Tinga, 2020	Imp	Yes	Yes
Titone, 2022	Exp	No	Not applicable
Tzvi, 2016	Imp	Yes	Yes
Wu, 2018	Imp	Yes	No

3.1.3. Awareness control

In studies on implicit motor sequence learning, it is essential to assess participants' level of awareness. Table 2 indicates which reviewed studies controlled for this factor. Awareness was generally assessed through self-report measures (Fujii et al., 2022; Lum et al., 2019, 2023b; Wu et al., 2018), tasks requiring participants to reproduce or explicitly generate the sequence (Lawson et al., 2017; Lum et al., 2023a, 2024; Rüsseler et al., 2003b; Tinga et al., 2020; Tzvi et al., 2016), recognition tasks (Dyck and Klaes, 2024), or multiple methods combined (Ferdinand et al., 2008; Lu et al., 2023). Some concerns have been raised regarding the sensitivity of self-report measures to identify participants with fully explicit knowledge. In particularly, fragmentary awareness, loss of knowledge at the moment of the report and inadequate contextual cues may limit the ability of these measures to accurately detect explicit awareness (Shanks and St. John, 1994; Gaillard et al., 2006). Forced choice measures, where participants see part of a sequence or must discriminate between seen/unseen sequences could provide higher sensitivity (Perruchet and Amorim, 1992; Shanks and St. John, 1994). However, this method also suffers from limitation, because the performance in such test could be influenced by the same implicit memory that the SRT is trying to assess (Perruchet and Amorim, 1992; Cohen and Curran, 1993; Destrebecqz and Peigneux, 2005). Alternative online assessment methods have been developed, based on the sudden decrease of reaction times during training, suggesting a change in behavior associated with explicit knowledge gain (Haider et al., 2005; Haider and Frensch, 2005; Haider and Rose, 2007). Furthermore, some authors found concordance between verbal reports and online behavioral measures, arguing for a reliability of verbal accounts (Haider et al., 2011). Considering strength and limitations, employing both self-report and objective measures, such as reproduction or recognition, is recommended, as it provides complementary qualitative and quantitative assessments of awareness.

3.2. EEG correlates of motor sequence learning

3.2.1. Event-related potentials

During motor sequence learning, changes in both latency and amplitude of medial frontal negativities (MFN) have been reported (Beaulieu et al., 2014; Matsuhashi et al., 2021). In particular within the MFN group, error-related negativity (ERN) is a component observed over central electrodes approximately 50 ms after an incorrect response and is associated with performance monitoring (Gehring et al., 1993; Botvinick et al., 2001). Correct-related negativity (CRN) is an ERN-like component, with similar topology and latency, occurring on correct trials (Coles et al., 2001) and is often interpreted as reflecting a subjectively perceived or partial error (Mathalon et al., 2002; Scheffers and Coles, 2000).

A study on implicit sequence learning (Beaulieu et al., 2014) reported that ERN amplitude during task execution was associated with accuracy, with greater amplitude being correlated to higher accuracy. Changes in ERN amplitude from the beginning to the end of the task correlated with sequence-specific learning gains, suggesting that increased ERN amplitude reflects improved learning. Additionally, shorter ERN latency was observed in participants who performed best at the end of the task, indicating anticipatory processes for upcoming movements. In contrast, Rüsseler et al. (2003b) found no difference in ERN amplitude between sequence and random trials, regardless of the learning block or participants' level of awareness.

In a study on explicit sequence learning, Matsuhashi et al. (2021) reported a correlation between movement improvements and MFN amplitude — particularly the CRN — suggesting that greater performance gains are associated with a more pronounced central negativity. However, these findings may not exclusively reflect sequence-specific learning, as general practice effects were not controlled. More generally, MFN shares similarities with frontal midline theta activity, which has been linked to error monitoring and cognitive control (Cavanagh and Frank, 2014). Following this interpretation, stronger MFN amplitude may also indicate a greater demand for cognitive control following an error. In summary, midline negativities are involved in both implicit and explicit motor sequence learning. They may signal a discrepancy from the internal sequence representation or reflect a greater need for cognitive control. However, further studies are required to clarify the functional role of these modulations, particularly in explicit sequence learning by including controls for general practice effects.

Contrasting results have been reported for the visual P1, N1, and P3 components. Visual P1 and N1 are typically observed 80–140 ms after stimulus onset over parietal-occipital electrodes and are generally associated with the allocation of visuospatial attention and stimulus processing (Hillyard and Anllo-Vento, 1998; Mangun and Hillyard, 1991). The P3 component, occurring approximately 300 ms after stimulus onset over parietal areas, has traditionally been linked to stimulus evaluation (Duncan-Johnson and Kopell, 1981), although later work questioned its specificity in distinguishing stimulus from response evaluation (Verleger, 1997). Other accounts interpret it mainly as reflecting context updating in response to deviant stimuli or, alternatively, marking the closure of a perceptual context (Altenmüller et al., 2005). More recently P300 has been associated to neural inhibition of ongoing activity to facilitate information transmission from working memory representational change to stimulus processing (Polich, 2007). Some studies reported P1 modulations during implicit sequence learning (Lum et al., 2019), with amplitude increase corresponding to learning gains, suggesting a gradual reduction in visuospatial attention demands over the course of the task. However, other studies using similar paradigms (Beaulieu et al., 2014; Fujii et al., 2022) failed to replicate these findings, indicating that changes in P1 may alternatively reflect fluctuations in arousal related to the experimental design.

An increase in N1 amplitude over time has also been reported, with significantly greater N1 observed in explicit learning compared to implicit learning (Lawson et al., 2017). Interestingly, the source of this component has been estimated to lie in the left precuneus, a region implicated in praxis and encoding of future intentions (Wenderoth et al., 2006; Wheaton et al., 2009), suggesting that the observed changes may reflect the formation of an internal representation linking visual stimulus to hand movements (Lawson et al., 2017). The P3 component was found to decrease over the course of the experiment regardless of awareness level, although its timing differed, occurring earlier in explicit learning. However, the absence comparisons with a control condition limited the ability to assess sequence-specific effects of these N1 and P3 findings. Additionally, other studies did not find significant changes in P3 or N1 (Fujii et al., 2022; Lum et al., 2019). The N2b component, found at 240–340 ms over frontal, central and parietal areas, typically elicited by violations of expectations (Eimer et al., 1996; Rüsseler et al., 2003a), was modulated when deviations were introduced to a learned sequence, but it did not change systematically with sequence learning (Ferdinand et al., 2008). Although all these components (P1, N1, P3, N2b) appear sensitive to stimuli that deviate from a learned sequence (Ferdinand et al., 2015, 2008; Rüsseler and Rösler, 2000; Schlaghecken et al., 2000), they do not appear to change as the sequence becomes automatized. In summary, the P1, N1, and P3 components do not exhibit consistent changes associated with motor sequence learning. Their modulation may depend on the participant's level of awareness of the sequence or on the presence of deviant stimuli.

Motor sequence learning has also been found to influence motor preparation, particularly the contingent negative variation (CNV) and contralateral delay activity (CDA). The CNV is a central negative deflection that follows a warning stimulus and precedes motor execution of about 200 ms (Jentzsch and Leuthold, 2002), whereas the CDA is a lateralized ERP with a posterior maximum, associated with the encoding of items in visual working memory (Klaver et al., 1999; Vogel et al., 2005). De Kleine and Van Der Lubbe (2011) reported higher central CNV amplitude when participants prepared to perform an unfamiliar sequence compared to a familiar one. Given that the difficulty level of

both sequence types was counterbalanced, this finding has been interpreted as a reduction in the complexity of motor preparation associated with learning. A similar pattern has been observed for the CDA over motor areas, which has been linked to visual working memory load (Klaver et al., 1999). This suggests that with practice, familiar sequences become more automatic, reducing the load on visual working memory. No differences were reported for the lateralized readiness potential (LRP), which generally reflects effector-specific motor preparation in M1 (Leuthold and Jentzsch, 2001). This aligns with other evidence indicating that only the first element of a sequence is prepared at an effector-specific level (Schröter and Leuthold, 2009), independent of sequence familiarity (De Kleine and Van Der Lubbe, 2011). In summary, motor sequence learning affects motor preparation by reducing its complexity, as indicated by lower CNV for learned stimuli, and by decreasing cognitive load, as reflected in lower CDA for learned sequences, whereas effector-specific activity measured by the LRP is not affected.

3.2.2. Brain oscillations

3.2.2.1. Theta. Theta oscillations over frontal-central and parietal areas have been linked to motor sequence learning. Specifically, a significant reduction in theta power from the early to later stages of the task has been observed for learned sequences (Lum et al., 2024; Tzvi et al., 2016), but not for random stimuli, which tend to show higher theta power (Lum et al., 2023b, 2024; Chatterjee et al., 2025), indicating sequence-specific effects. In implicit motor sequence learning, this reduction in theta oscillations has been interpreted as reflecting a decreased need for attentional resources as the task becomes more automated (Lum et al., 2024, 2023b; Tzvi et al., 2016). Studies on probabilistic sequence learning (Ambrus et al., 2020; Park et al., 2022; Tóth et al., 2017), where sequence awareness is better controlled, have shown that performance can be hindered by goal-directed (top-down) processes, implying that weaker top-down control and stronger bottom-up processes may facilitate implicit learning. Similar mechanisms have been proposed for deterministic sequence learning, in which excessive top-down control could interfere with the detection of regularities in sensory input (Lum et al., 2024). Additionally, theta activity positively correlated with behavioral measures, with higher theta associated to greater block reaction times (Lum et al., 2024). Midline theta synchronization has been proposed to reflect a neural mechanism signaling the need for enhanced cognitive control under conditions of uncertainty (Cavanagh and Frank, 2014), supporting behavioral adaptation to contextual demands. This signal is thought to originate in the midcingulate cortex and pre-supplemental motor area, with the midcingulate cortex acting as a hub connecting cortical and subcortical regions (Cohen, 2011) and entraining distributed neural systems (Cavanagh and Frank, 2014). In the context of motor sequence learning, the reduction in midline theta activity over time likely reflects increased predictive processing based on acquired sequence knowledge, thereby reducing the demand for cognitive control. Other accounts showed higher frontal activity in fixed sequence when participants gain explicit knowledge of the regularity, but not in sessions where participants were performing the task implicitly or once they gained full awareness (Lu et al., 2023). By adopting the same framework, we could interpret this finding as increased cognitive demand when regularity is being discovered. Regarding parietal areas, theta activity was higher for sequence stimuli than for random stimuli during the early stages of implicit learning, but this difference disappeared in later stages (Tzvi et al., 2016). Similarly, higher parietal theta was reported for sequence during implicit learning before gaining sequence awareness (Lu et al., 2023). These findings may reflect the engagement of working memory processes (Roux and Uhlhaas, 2014), with greater attentional demands required at the beginning of learning, when the information to maintain is larger. Alternatively, this pattern may reflect the acquisition of sequence knowledge, as indicated by the parietal-to-frontal transfer of theta activity observed in the phase transfer entropy analysis of the same study (Lu et al., 2023).

In summary, midline theta activity is associated with sequence-specific learning and may reflect mechanisms of top-down cognitive control, with a progressive reduction in the need for control as learning advances. Evidence regarding parietal theta activity shows a potential role in working memory processes.

3.2.2.2. Alpha. Findings on alpha activity suggest that its modulation primarily reflects changes in neural efficiency within task-relevant areas, rather than processes specific to sequence learning. Across both explicit and implicit sequence learning tasks, increases in alpha power over parietal-occipital (Tinga et al., 2020) and left temporal regions (Bellomo et al., 2018) during task performance have been reported. However, in both studies, alpha modulations were observed across experimental conditions and are generally interpreted as practice-related effects rather than sequence-specific learning. Within the framework of the functional inhibition theory (Jensen and Mazaheri, 2010) — which posits that alpha synchronization reflects the functional inhibition of task-irrelevant regions — such an increase may indicate more efficient allocation of neural resources during task execution. In line with this account, Hummel et al. (2003) reported decreased alpha power in bilateral sensorimotor and frontal-central areas when participants performed sequences requiring high-level motor skills compared to simple movements. This effect was observed regardless of whether the sequence was pre-learned or novel, further supporting the interpretation that alpha modulation indexes general task demands and general practice-related activity rather than sequence learning per se. However, it is difficult to exclude the possibility that the observed practice-related increases in alpha power may be partially attributable to mental fatigue, which has also been associated with enhanced alpha activity (Tran et al., 2020).

While most evidence points to a non-specific role of alpha activity, some studies suggest a more task-specific, anticipatory function. In implicit sequence learning, some studies found differential alpha modulation between sequence and random stimuli. For instance, Lum et al. (2023b) observed a general increase in alpha activity across the task over frontal, central and parieto-occipital areas, whereas Lum et al. (2024) reported that pre-response alpha power in the contralateral motor area decreased progressively with repeated sequence trials and increased when performing random sequence. However, no correlation has been found between alpha power and sequence specific behavioral measures, likely reflecting more general neural optimization during motor learning. These findings point to a shift of resource allocation, with reduced resources needed to process visual input and increased relevance of motor preparation as the sequence is well established. Conversely, alpha power was found to be higher when processing sequences at the beginning of the task but lower at later stages, compared to random stimuli, over central and parietal-occipital regions (Tzvi et al., 2016). This result seems to be at odd with the other reviewed findings, further studies are necessary to clarify the relationship between alpha modulation and learning over time.

In summary, alpha activity increases in motor and parietal areas with task progression and desynchronizes with higher sequence complexity. Overall, these changes are more consistently explained by general practice-related effects, reflecting more efficient allocation of neural resources for stimulus prediction and motor planning as task familiarity increases. Although alpha activity can show sequence-specific modulations, such changes are more consistently explained in terms of ongoing neural optimization by activating task-relevant regions and inhibiting task irrelevant ones.

3.2.2.3. Beta. Beta activity has been predominantly observed over motor and parietal areas and associated with sensorimotor processes.

Pre-movement beta activity shows learning-related modulation in motor (Lum et al., 2024; Chatterjee et al., 2025) and parieto-occipital areas (Lum et al., 2023b) during both implicit and explicit learning. In implicit motor sequence learning, pre-movement beta over motor areas decreases progressively with sequence repetition, paralleling faster reaction times, and increases during random sequences (Lum et al., 2024). According to Engel and Fries (2010), an increase in beta power may indicate the maintenance of the current motor and cognitive set, associated with stronger endogenous top-down control, whereas beta desynchronization signals a shift in the set, promoting flexibility and bottom-up processing. By applying this framework, the reported pre-movement beta decrease may facilitate bottom-up detection of regularities, whereas the increase observed during random trials may reflect attempts to generate predictive responses based on prior experience. Multiple studies have reported beta desynchronization during motor execution (Chatterjee et al., 2025; Dyck and Klaes, 2024; Hummel et al., 2003; Mottaz et al., 2024), a phenomenon well-documented in motor control research (Engel and Fries, 2010; Kilavik et al., 2013). Notably, the degree of beta suppression at the beginning of training has been found to correlate with learning gains, supporting the hypothesis that beta activity plays a role in cortical reorganization that facilitates motor learning (Dyck and Klaes, 2024; Pollok et al., 2014). A general increase in beta activity over the course of training has also been reported (Dyck and Klaes, 2024), although the extent of this increase is modulated by the presence of both implicit and explicit sequences. Specifically, beta activity tends to be higher over contralateral motor areas once the sequence has been acquired through repeated practice sessions (Dyck and Klaes, 2024). In contrast, a general decrease in parieto-occipital beta power during response has been observed regardless of sequence condition, suggesting a general practice effect (Lum et al., 2023b). While the precise functional role of beta oscillations remains debated, they are generally considered to reflect sensorimotor processes. Following Engel and Fries (2010), the increase in beta power during motor learning may reflect the maintenance of a motor plan as familiarity grows, particularly when the plan involves a repeated sequence. A similar interpretation applies to findings of Hummel et al. (2003), who observed stronger beta desynchronization over motor areas during the performance of a complex sequence task compared to simple key presses, regardless of learning status, suggesting the need for a more flexible motor plan. Post-response beta activity is modulated also by temporal uncertainty (Li et al., 2026). When the onset timing of a stimulus is fixed and predictable, beta power shows a linear decrease facilitating motor readiness. However, when uncertainty about stimulus onset is introduced and the predictability is lower, the beta attenuation curve is less stable, suggesting a shift from a top-down control to a more stimulus-driven pattern (Li et al., 2026). A final piece of evidence associates frontal beta activity with the emergence of sequence awareness, as suggested by Lu et al. (2023).

Overall, beta activity appears to be modulated by both general practice and sequence-specific learning before, during and after movement (Dyck and Klaes, 2024; Lum et al., 2023b; Chatterjee et al., 2025). Individual learning strategies also appear to influence beta patterns. Distinct patterns of beta-band modulation have been observed both in controlled settings (Pollok et al., 2014) and in real-world tasks (Haar and Faisal, 2020), supporting the idea of strategy-specific neural dynamics (Barone and Rossiter, 2021). Furthermore, activity in the low and high beta bands may reflect distinct neurophysiological mechanisms. Animal studies have linked low beta (<20 Hz), originating from M1, to motor control, with positive correlations reported between low-beta power and reaction times during movement preparation. In contrast, high beta activity (>20 Hz), originating from the premotor cortex, has been associated with spatiotemporal attention and is modulated by anticipation and visual cues, but not by reaction times (Nougaret et al., 2024). A similar dissociation was observed in a motor adaptation task, where low beta was modulated by kinematic errors and high beta by outcome feedback (Schwey et al., 2023). These findings suggest that beta activity in motor sequence learning serves multiple functions and originates from distinct sources. Beta activity is also modulated by stimulus temporal and spatial uncertainty (Palmer et al., 2019; Schmidt-Kassow et al., 2023; Li et al., 2026), making this an additional methodological factor to consider. Given the impact of all the variables discussed above, discrepancies across studies may relate to differences in stimulus uncertainty, task design, sequence awareness, or sequence complexity. Future research should aim to disentangle these contributions and explore different patterns of beta modulation.

In summary, beta activity generally increases across learning, potentially reflecting the maintenance of current motor and cognitive plans, particularly in the context of repeated sequences. During learning, pre-movement beta decreases over motor areas supporting bottom-up processes, whereas it increases during movement execution reflecting maintenance of the motor plan as the sequence is acquired. Beta modulations are influenced by different factors such as stimulus predictability, sequence complexity, and individual learning strategies.

3.2.2.4. Gamma. Gamma activity has been found in one study to be higher during early stages of learning over parietal areas and to decrease in later stages (Tinga et al., 2020). This pattern was observed across experimental conditions, suggesting a general practice effect rather than a sequence-specific effect. However, higher gamma activity for sequence trials compared to random trials have been reported, pointing to a potential role in sequence-specific learning. Notably, this study did not report significant changes in gamma power over time. Gamma oscillations have been proposed to reflect modulations of synaptic plasticity, and their magnitude has been associated with learning across various tasks, particularly in working memory encoding (Nowak et al., 2018). Despite this, few studies have specifically investigated gamma power changes in motor sequence learning, partly due to methodological challenges, including its susceptibility to artefacts (O'Donnell et al., 1974; Whitham et al., 2008; Hipp and Siegel, 2013). When considered, gamma activity was often examined in the context of cross-frequency coupling — typically with lower-frequency bands such as theta — to explore long-range communication across brain networks (Nowak et al., 2018).

In summary, gamma-band activity remains under-investigated in the context of motor sequence learning. A general decrease in gamma power over parietal areas has been reported during implicit sequence learning, while some evidence suggests that gamma oscillations may play a sequence-specific role in encoding.

3.3. Functional connectivity and motor sequence learning

Functional connectivity enables the investigation of interactions among distributed brain regions, particularly when communication unfolds in complex, large-scale networks. Although studies adopting this approach in motor sequence learning are still limited and heterogeneous, available evidence points to learning-related changes in connectivity among the brain regions discussed so far.

Alpha-band functional connectivity between frontal and temporal regions appears to be modulated during sequence learning. In particular, a decrease in interhemispheric frontal-temporal phase-locking value (PLV) following implicit learning training has been found to be associated with behavioral learning gains, possibly indicating a shift toward more localized, task-specific processing (Farrokhi et al., 2025). Consistently, within the same hemisphere, an increase in high-alpha connectivity between frontal and temporal regions has been observed over time in both implicit and explicit learning, which has been interpreted as reflecting co-inhibition between these areas (Bellomo et al., 2018). However, the lack of control conditions in this study limits conclusions regarding sequence-specificity.

Additional networks modulated by learning include right frontocentral and fronto-parietal circuits. In fact, a decrease in alpha-gamma

phase-amplitude coupling (PAC) has been observed during the execution of implicitly learned sequences relative to random stimuli (Tzvi et al., 2016). Interestingly, this communication pattern may extend to random blocks immediately following a sequence block, though not to other random blocks, and is accompanied by poorer behavioral performance, suggesting that the learned sequence continues to be implicitly implemented for a short time after the sequence block (Tzvi et al., 2016).

Learning-related connectivity modulations within fronto-central and fronto-parietal networks have also been observed in the beta band, typically showing left hemisphere lateralization in right-hand tasks. Within the left hemisphere, lower high-beta PLV has been reported for sequence compared to random stimuli, suggesting a reduced engagement of top-down attentional resources once the sequence is learned (Fujii et al., 2022). During motor preparation, a reduction in beta-band coherence between the left M1 and the left parietal cortex has been reported with practice, and these changes have been shown to predict improvements in motor performance, though not motor learning itself (Wu et al., 2018). Moreover, coherence peaked at different time points across M1, right prefrontal, and left parietal areas, highlighting the importance of temporal dynamics in functional connectivity during learning (Wu et al., 2018). Additional evidence indicates that beta-range connectivity within frontal-central and parietal-temporal areas decreases by the end of training but increases following a declarative task, suggesting that suppressing declarative memory processes may facilitate implicit learning consolidation (Farrokhi et al., 2025). Beta connectivity changes have also been reported within the medial temporal lobe. In particular, connectivity was found to decrease immediately after training, and connectivity levels during training predicted motor sequence learning outcomes independently of awareness (Mottaz et al., 2024).

Resting-state gamma-band connectivity has also been observed between motor areas and ventral attention and language networks in explicit sequence learning, possibly reflecting a reduced reliance on cognitive control once the sequence has been consolidated (Titone et al., 2022). Taken together, these findings indicate the involvement of motor-parietal, fronto-parietal and fronto-temporal networks in motor sequence learning, mostly associated with general practice effects rather than sequence-specific learning. These networks have been shown to play a role in motor planning and eye-hand visuomotor integration (Battaglia-Mayer et al., 2015; Borra and Luppino, 2019), processes that are engaged in the tasks of all the reviewed studies.

Overall, a general reduction in connectivity during training appears to be predictive of better performance, favoring more efficient processing within specialized brain areas. This is consistent with evidence from EEG (Gentili et al., 2015; Manuel et al., 2018; Mottaz et al., 2024) and fMRI studies (Coynel et al., 2010; Karim et al., 2017; Wu et al., 2008). The role of frontal, motor, parietal and temporal areas in motor sequence learning has been reported in different fMRI studies (Hardwick et al., 2013; Byczynski et al., 2025;), with some subcortical areas critically accounting for sequence specific effects, such as basal ganglia (Janacsek et al., 2020). Even if activity originating from subcortical areas cannot be directly recorded with EEG, their contribution to cortical activity has been established (Tan et al., 2014; Seeber et al., 2019). Further studies employing appropriate control conditions and robust behavioral measures are required to clarify the contribution of connectivity changes to sequence-specific motor learning.

In summary, functional connectivity studies indicate that communication in alpha and beta bands within motor–parietal, fronto–parietal, and fronto–temporal networks changes with practice. While sequence-specific effects are rarely reported, some evidence suggests a potential role for alpha-gamma PAC between frontal-central and parietal regions in sequence processing. Nevertheless, additional studies with rigorous control conditions are needed to confirm these findings and to disentangle learning-related effects from general practice-related changes.

3.4. Resting-state predictors of motor sequence learning

Several studies have examined resting-state oscillatory activity prior to task execution to assess its predictive value for motor sequence learning.

In the theta band, resting-state midline activity has been associated with implicit sequence learning, with lower resting theta predicting greater training-related gains (Lum al., 2023a). This finding is consistent with previous evidence suggesting that excessive top-down attentional control may interfere with implicit learning processes. In explicit motor sequence learning, resting-state connectivity in the theta and also delta bands between motor regions and areas belonging to the visual network – ventral and dorsal attentional networks and default mode networks has been found to correlate with learning outcomes (Titone et al., 2022).

In the alpha band, increased functional connectivity within motor regions has been significantly linked to better learning performance (Mottaz et al., 2024). Conversely, lower resting-state alpha connectivity within the striatum, assessed through source analysis, has been associated with long-term expertise, while post-task increases in striatal alpha connectivity have been correlated with enhanced consolidation. Alpha power has not been reported as predictive of training related changes (Lum et al., 2023a; Mottaz et al., 2024).

Higher whole-brain and motor-premotor beta-band coherence at rest has also been linked to better learning-related outcomes (Wu et al., 2018). Beta oscillations have been proposed to play a role in short-term consolidation processes (Pollok et al., 2014); however, lower baseline beta connectivity between motor areas and visual/attentional networks has been associated with greater offline learning gains (Titone et al., 2022). These findings suggest that resting-state beta connectivity may be a more reliable predictor of learning than absolute beta power, which has yielded inconsistent results across studies (Lum et al., 2023a; Sugata et al., 2020). Also for beta band, resting state power does not seem predictive of learning related changes (Lum et al., 2023a; Mottaz et al., 2024).

In summary, resting-state neural activity prior to motor sequence learning can predict subsequent performance and learning outcomes, particularly with respect to midline theta power and motor-premotor beta coherence. Connectivity in the beta and alpha bands — especially within motor areas and the striatum — may also predict long-term learning and consolidation, although these effects may partly reflect general practice-related processes. Further research is needed to clarify the specificity of these resting-state markers to sequence learning and to disentangle them from broader motor learning mechanisms.

The main EEG findings about baseline resting state and training related changes have been summarized in Fig. 3.

4. Comparison of EEG correlates of motor sequence learning and sensorimotor adaptation

Numerous studies included in this review have demonstrated significant EEG modulation associated with cognitive processes that are also implicated in other forms of motor learning. In particular, sensorimotor adaptation represents another well-studied domain of motor learning research. The recent review by Reuter et al. (2022) provides an opportunity to compare EEG findings across these two forms of motor learning.

In both forms of learning, modulations of ERN have been shown, indicating changes in error monitoring processes during learning. In motor sequence learning, ERN modulations are thought to reflect discrepancies in the internal representation of the sequence as well as increased cognitive demands. Similarly, in sensorimotor adaptation, the ERN is modulated by trajectory-related feedback during movement execution and, when evoked by task feedback, to strategic control processes. The latter function may also be relevant to motor sequence learning, as it is not linked to the nature of the movement itself but rather to its outcome. In contrast, changes in the P300 have not been

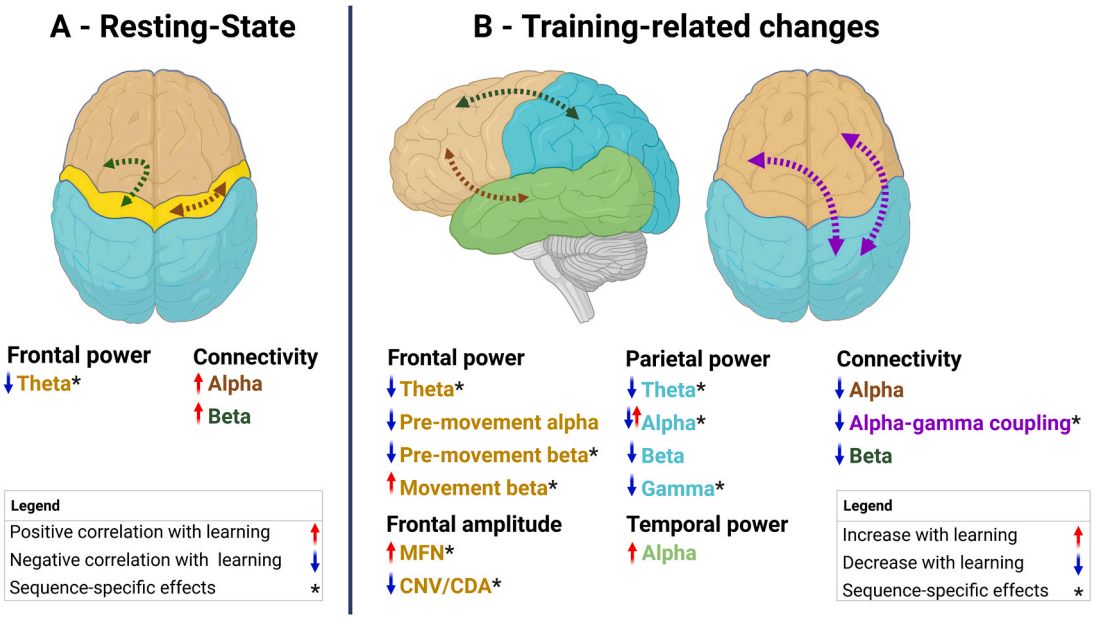


Fig. 3. Resting-state and training-related EEG main findings. *Panel A* summarizes pre-training resting-state EEG measures associated with subsequent motor learning performance. Colored arrows below the brain schematics indicate the direction of the correlation between EEG measures and learning improvements: red arrows indicate a positive correlation (higher power or connectivity measure predicts greater learning); blue arrows indicate negative correlations (lower power or connectivity measure predicts greater learning). Dashed arrows connecting cortical regions in the brain schematics represent connectivity findings between those areas and do not imply anatomical directionality or causal information flow. *Panel B* summarizes EEG changes observed during the training phase of motor sequence learning. Colored arrows below the brain schematics indicate the direction of EEG changes during learning: red arrows indicate increases in power or connectivity for frequency bands (or amplitude for event-related potentials); blue arrows indicate decreases associated with improved behavioral performance. Dashed arrows connecting cortical regions in the brain schematics represent connectivity findings between those areas and do not imply anatomical directionality or causal information flow.

Text labels are color-coded to match the cortical regions highlighted in the brain schematics, reflecting the cortical areas associated with the EEG effects reported in the reviewed studies. When colors are associated with cortical regions (Frontal, Parietal, Temporal), they indicate the EEG effects observed in those at areas; when they refer to connectivity measures, they indicate the EEG effects associated with the specific connections represented by dashed arrows. Asterisks indicate sequence-specific effects, namely EEG measures that showed significant differences between fixed-sequence and control conditions. Created in BioRender. Falciati, L. (2026) https://BioRender.com/9mqxezj.

consistently reported in motor sequence learning, whereas in sensorimotor adaptation this component is reliably modulated by error magnitude.

Theta activity is modulated in both sequence learning and sensorimotor adaptation, particularly over frontal and parietal regions. In motor sequence learning, frontal-central theta shows sequence-specific reductions as the fixed movement pattern is acquired, likely reflecting a decreased demand for top-down control. In sensorimotor adaptation, theta displays distinct modulation patterns before and after movement execution. In particular, post-movement theta, also investigated in sequence learning (Lum et al., 2024), shows a similar decrease during adaptation (Arrighi et al., 2016; Fine et al., 2017; Jonker et al., 2021; Kooiman et al., 2020) and during the acquisition of novel strategies (Savoie et al., 2018). This convergence suggests a common role of post-movement theta in signaling the need for cognitive control to suppress outdated motor plans and implement more adaptive ones (Reuter et al., 2022). Pre-movement theta in motor sequence learning shows higher power when random stimuli are presented following training on a fixed sequence (Lum et al., 2023b), a pattern consistent with that observed for post-movement theta. In contrast, studies of sensorimotor adaptation have reported an increase in pre-movement theta over the course of learning, suggesting a growing involvement of strategic processes during movement planning (Reuter et al., 2022). This discrepancy may reflect differences in motor preparation demands between the motor sequence learning tasks included in this review, which primarily involve button presses, and the adaptation paradigms (Gentili et al., 2011; Novakovic and Sanguineti, 2011; Perfetti et al., 2011), which require more complex motor actions. Finally, parietal theta in motor sequence learning exhibits sequence-specific effects that have been linked to greater working memory engagement during the early stages of learning, while in sensorimotor adaptation it appears to support motor remapping following sensory prediction errors.

Alpha activity shows a similar trend in both forms of motor learning, with higher synchronization over the course of learning. In both cases, this pattern appears to reflect neural efficiency: in motor sequence learning, through more efficient stimulus processing and motor preparation, and in sensorimotor adaptation, through reduced demands on movement control and greater resource allocation to movement preparation.

Beta activity is modulated differently across motor sequence learning and sensorimotor adaptation depending on whether it is measured before, during or after movement execution. In motor sequence learning, pre-movement beta decreases as the sequence is acquired (Lum et al., 2024), potentially facilitating bottom-up detection of regularities. In contrast, pre-movement beta modulation in sensorimotor adaptation has been linked to the processing of afferent somatosensory information elicited by sensory prediction errors. During response execution, movement-related beta desynchronization shows opposite patterns in the two learning paradigms: during motor sequence learning, beta power increases with learning (Dyck and Klaes, 2024), while in sensorimotor adaptation stronger beta desynchronization is observed as adaptation progresses (Rustighi et al., 2010; Kooiman et al., 2020). These divergent findings may reflect differences in the nature of the movements and sensorimotor information involved in the two forms of learning. Nevertheless, similar connectivity patterns have been reported in both tasks, with beta-band connectivity decreasing as learning progresses, suggesting a reduced reliance on widespread cortical networks. Post-movement beta rebound has been investigated more extensively in

sensorimotor adaptation than in motor sequence learning. Converging evidence indicates that beta rebound is sensitive to information uncertainty, with its modulation potentially supporting either top-down control or bottom-up adaptation strategies depending on task demands and performance outcomes.

Learning-related changes in gamma activity have also been reported in both motor sequence learning and sensorimotor adaptation, generally taking the form of a decrease in gamma power as learning progresses (Tinga et al., 2020;Perfetti et al., 2011; Wong et al., 2014; Kooiman et al., 2020). However, in both domains, the functional significance of gamma oscillations remains difficult to establish. This uncertainty is further compounded by methodological challenges associated with EEG recordings in the gamma bands (O'Donnell et al., 1974; Whitham et al., 2008; Hipp and Siegel, 2013), which may limit the interpretation of reported findings.

Overall, comparison with the sensorimotor adaptation literature suggests that many EEG signatures index processes that are shared across both forms of learning, including error monitoring, modulation of cognitive control, and increasing neural efficiency. Learning-related changes in these processes may therefore reflect common mechanisms underpinning general motor learning. Some of the observed similarities may also arise from partial overlap between the two forms of learning within experimental paradigms. Indeed, tasks designed to isolate one learning process may still engage elements of the other; for example, sequence learning tasks can involve adaptive sensorimotor adjustments, whereas adaptation tasks may recruit sequencing-related processes. Conversely, the differences observed between the two domains are more likely to reflect variations in movement complexity and sensorimotor demands than fundamentally distinct learning mechanisms. Nevertheless, the functional significance of some EEG markers, particularly gamma-band activity, remains unclear and warrants further investigation.

5. Study limitations and future directions

This paper aimed to synthesize existing findings on the EEG correlates of deterministic motor sequence learning, with a particular focus on disentangling sequence-specific effects from general practice-related changes. A major limitation of the reviewed literature is the heterogeneity of the studies, particularly regarding the measures employed, the experimental paradigms, and the limited replication of findings. This heterogeneity reduces comparability and generalizability, making it difficult to draw a coherent picture. Another key limitation is the frequent absence of appropriate control conditions for general practice effects, especially in studies employing explicit learning paradigms. The inclusion of such control conditions is essential to prevent conflating learning-related EEG modulations with nonspecific improvements in stimulus-response mapping or motor execution. The exclusion of MEG studies and intracranial EEG, which hold better spatial resolution compared to surface EEG, is another limitation of this study. In particular, these techniques can access subcortical areas, such as basal ganglia, hippocampus and cerebellum, that have a role in motor sequence learning (Chen et al., 2025; Herrojo Ruiz et al., 2014; Kornysheva et al., 2019; Sugata et al., 2025). EEG's lack of accurate spatial information does not allow to directly compare results with fMRI literature and integrate the findings. Source reconstruction methods, even if show some limitations, have been rarely applied to motor sequence learning. Another limitation of this review is the exclusion of studies employing statistical learning paradigms. Such tasks are particularly well suited to dissociate general practice effects from sequence-specific learning, as they manipulate graded levels of sequence predictability (Janacsek and Nemeth, 2012). In addition, some statistical learning paradigms incorporate methodological features that minimize participants' awareness of the underlying regularities, making them especially suitable for investigating implicit learning processes (Janacsek and Nemeth, 2012). However, these studies fell outside the scope of the present review, which focused specifically on EEG changes associated with the acquisition of fixed, well-defined motor sequences, rather than the learning of probabilistic regularities that typically characterize statistical learning paradigms.

Future research is required to further investigate and strengthen the current understanding of motor sequence learning. Extending evidence on brain connectivity would be valuable to achieve a more comprehensive characterization of the neural networks involved. Further studies employing source reconstruction methods are needed to improve spatial localization accuracy and to enhance comparability with findings obtained using other techniques, such as MEG and fMRI. Different analysis approaches could be applied to investigate sequence learning, and machine learning models may provide valuable insights as well as support the testing of specific hypothesis (eg. Kornysheva et al., 2019; Arun et al., 2021; Han et al., 2025). Another direction for EEG research on motor sequence learning is to further advance knowledge and findings within recently developed theoretical frameworks. A possible direction for future work could be differentiate the EEG markers underlying the "what" and "how" aspects of motor sequence learning, i.e. anticipating which movements to perform and optimizing their execution within the sequence (Kashefi et al., 2025). Evidence for the former has been found (Wong et al., 2015); however, both aspects have been shown to contribute significantly to improvements in motor learning (Kashefi et al., 2025). Some of the reviewed evidence appears to partially suggest improved stimulus prediction and enhanced motor preparation during sequence learning; however, studies using this paradigm are necessary to disentangle these processes. Furthermore, an intermediate hierarchical level between action selection and execution has been proposed (Diedrichsen and Kornysheva, 2015) that may play a role in skill learning and could therefore be worth investigating. Another theoretical framework is the competitive queuing models (Lashley, 1951; Rhodes et al., 2004), which proposes a layer in which multiple plan representations can be active simultaneously. The most active plan is selected for execution based on activation-based competition and is then removed from the planning layer before the competition is reinitiated. None of the included studies in this review directly addressed this issue; therefore, future work is needed to test this hypothesis, in particular by investigating neural changes during preparation in sequence learning using ad hoc experimental design, as recently done in a MEG study (Kornysheva et al., 2019).

6. Conclusions

The present review summarizes the main EEG findings associated with deterministic motor sequence learning. The examined literature is characterized by substantial methodological and analytical heterogeneity, which limits the comparability and generalizability of the results. Across different experimental and analytical approaches, findings are inconsistent and inconclusive, so further research is needed to corroborate and replicate much of the existing evidence. While a relatively large body of evidence was collected on time-domain and frequency-domain measures, investigations on connectivity measures are scarce. As a consequence, our understanding of neural dynamics underlying motor sequence learning is still partial and limited to a restricted set of works.

Among the time-domain analyses considered, only midline frontal negativities consistently appear to be associated with motor sequence learning. These components, irrespective of the level of awareness, are likely involved in performance monitoring and error processing. CNV and CDA are modulated when executing learned sequences compared to unfamiliar ones, suggesting learning-related changes in motor preparation and working memory demands. In contrast, other ERP components, such as N1, P3, and N2, do not show consistent temporal modulations that can be reliably attributed to motor sequence learning.

Across reviewed studies, time-frequency analyses consistently identify changes in midline theta activity as being associated with motor

sequence learning. These changes are likely to reflect a progressive reduction in top-down attentional demands and cognitive control requirements as the sequence becomes automatized. By contrast, changes in alpha activity are generally not sequence-specific and instead appear to reflect general training-related increases in neural processing efficiency. Although some studies report sequence-specific changes in parietal alpha activity, these findings remain inconclusive and require further replication. In the beta band, a limited number of studies describe sequence-specific effects; however, these results are inconsistent and appear to be strongly influenced by task design awareness, and substantial inter-individual variability. Evidence regarding gamma-band activity is sparse, but available findings suggest a potential role in sequence learning, possibly related to plasticity mechanisms in parietal areas.

Functional connectivity studies remain relatively scarce but provide valuable insights into learning-related changes in communication between brain networks. For instance, alpha-gamma phase-amplitude coupling within frontal-parietal areas has been found to increase during sequence execution. Additionally, connectivity changes involving motor, premotor, prefrontal, and temporal areas have been associated with learning, although their specificity to sequence-learning, as opposed to general practice effects, has not yet been clearly established.

Resting-state EEG studies further provide evidence that baseline theta power activity and beta-band connectivity, especially between motor and premotor areas, can predict training-related improvements in motor sequence learning. Moreover, alpha- and beta-band connectivity within motor and striatal regions may contribute to consolidation processes and long-term skill retention.

Overall, EEG markers of motor sequence learning need further investigation, with particular attention to the inclusion of appropriate control conditions that allow for a clear dissociation between general practice-related changes and sequence-specific learning effects, in both implicit and explicit learning paradigms.

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Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used ChatGPT 4.1 by OpenAI to improve the language and readability of the manuscript. Following this, the authors carefully reviewed and edited all content as needed and took full responsibility for the published work.

Declaration of Competing Interest

The authors declare no competing interests.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neubiorev.2026.106873.

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