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Behavioral and neural markers of serial order and timing in skilled motor sequences during planning

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Behavioral and neural markers of serial order and timing in skilled motor sequences during planning

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This thesis is submitted in partial fulfilment of the requirement for the degree of Doctor of Philosophy, completed in the school of Psychology, Bangor University

Declaration

‘I hereby declare that this thesis is the results of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards.

I confirm that I am submitting this work with the agreement of my Supervisor(s).’

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‘Yr wyf drwy hyn yn datgan mai canlyniad fy ymchwil fy hun yw’r thesis hwn, ac eithrio lle nodir yn wahanol. Caiff ffynonellau eraill eu cydnabod gan droednodiadau yn rhoi cyfeiriadau eglur. Nid yw sylwedd y gwaith hwn wedi cael ei dderbyn o’r blaen ar gyfer unrhyw radd, ac nid yw’n cael ei gyflwyno ar yr un pryd mewn ymgeisiaeth am unrhyw radd oni bai ei fod, fel y cytunwyd gan y Brifysgol, am gymwysterau deuol cymeradwy.

Rwy'n cadarnhau fy mod yn cyflwyno'r gwaith hwn gyda chytundeb fy Ngoruchwyliwr (Goruchwylwyr)

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Στον Πέτρο

Summary

The ability to organize our movements in well-coordinated and functional sequences that are flexibly retrieved and generated from memory is a hallmark of the human behavioral repertoire. To achieve this skill, the brain utilizes the period before movement initiation to 'set up' and prepare the key higher-order properties of sequence representation, namely the order and timing of sequential movements. Previous neurophysiological research provides evidence for a parallel graded preactivation of upcoming movements offering support for a class of neural network models, termed competitive queuing (CQ). Timing has been modelled in this context as a key regulator of ordinal position of to-be-performed movements, whilst preparation time has been associated with improved subsequent performance. What remains unanswered is the role of preparation time and sequence timing in preorganizing the previously reported gradient of movements according to their position in the sequence during planning. By addressing that question, the present thesis aimed at disambiguating the representation of serial order and sequence timing during planning both with behavioral and neural measures. With a novel behavioral 'delayed-production' paradigm which utilized movement probes, this thesis first investigated the behavioral readout of the CQ mechanism prior to execution of well-learnt finger sequences and its modulation by preparation time or sequence timing (different speeds/temporal grouping). Subsequently, using movement decoding from non-invasive Electroencephalography (EEG) and concurrent Electromyography (EMG), the parallel graded preactivation of upcoming movements and the potential impact of sequence timing, and specifically different speeds, on regulating the preactivations were further examined. The findings revealed that the preparatory CQ gradient acquired at the behavioral level represented the serial order of simultaneously prepared movements depending on their initial position in the sequence. The quality of movements' organization expressed via the CQ gradient during planning was improved by more time to prepare the sequence, not its timing. The longer the preparation time the more the gradient was expanded refining the movements' organization by their ordinal position. When more pronounced, i.e., featuring more distinct differences between positions, the gradient predicted better sequence performance, suggesting that this mechanism supports a more accurate sequence plan accounting for improved sequence execution. The preparatory CQ gradient also reflected a fine-grained mechanism which determines the preparatory state of movements depending on whether a planned movement belongs to a sequence or not, or whether a movement is planned as part of a sequence or not. In contrast to previous findings, time-resolved EEG decoding showed that movement-related neural patterns were not preactivated in parallel before execution. Post hoc transformation of both the EEG and the EMG time series and timing analysis demonstrated that the EEG signal was scaled during sequence planning according to the speed of the cued sequence. The timing of a movement unrelated to the planned sequence was rehearsed during sequence planning at the same time as the sequential movement in the first position. Both findings were not present at the neural periphery during sequence planning suggesting a high-level timing rehearsal of upcoming movements in the absence of overt motor behavior. Overall, these findings demonstrate that order and timing are controlled by different mechanisms during the planning of skilled motor sequences. This research has implications for understanding a modular control of motor sequence representation and the planning dynamics through different modalities and measures. Finally, these findings are discussed in reference to skilled sequencing in movement disorders.

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Acronyms & Abbreviations

ANOVA ……	Analysis of variance
BCI …….....	Brain-computer interface
BG …….....	Basal ganglia
BEM …….....	Boundary element method
BOLD …….....	Blood oxygenation level-dependent
CQ …….....	Competitive queuing
DLPFC …….....	Dorsolateral prefrontal cortex
EEG …….....	Electroencephalography
EMG …….....	Electromyography
ERD ……	Event-related desynchronization
ERS ……...	Event-related synchronization
fMRI …….....	Functional magnetic resonance imaging
Hz ……	Hertz
ICA …….....	Independent component analysis
IPI …….....	Inter-press interval
ISR …….....	Immediate serial recall
ITI …….....	Inter-trial interval
LDA …….....	Linear discriminant analysis
LRP …….....	Lateralized readiness potential
LSTM …….....	Long short term memory
LTM …….....	Long-term memory
M1 …….....	Primary motor cortex
MEG …….....	Magnetoencephalography
MEP …….....	Motor evoked potentials
mm …….	Millimeter
MNI …….....	Montreal Neurological Institute
ms …….....	Millisecond
MVPA …….....	Multi-voxel pattern analysis
PhG …….....	Parahippocampal gyrus
PMd …….....	Dorsal premotor cortex
pre-SMA …….....	Subdivision of the anterior supplementary motor area
RCF …….....	Recurrent competitive field
RNN …….....	Recurrent neural network
ROI …….....	Region of interest
RT …….....	Reaction time
s …….....	Second
S1 …….....	Primary somatosensory cortex
SMA …….....	Supplementary motor area
STM …….....	Short-term memory
SWR …….....	Sharp-wave ripple
WM …….....	Working memory

Published Work & Dissemination of Research

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Mantziara, M., Ivanov, T., Houghton, G., & Kornysheva, K. (2020, March). *Competitive queuing state of actions during planning predicts execution accuracy of a motor sequence* [Poster presentation]. Cognitive Neuroscience Society (CNS) 2020 Annual Meeting, Virtual.

Mantziara, M., Ivanov, T., Houghton, G., & Kornysheva, K. (2019). *Competitive queuing of actions during sequence preparation reflects preparation time, but not sequence timing* [Poster presentation]. UK Sensorimotor Conference 2019, London, UK.

Manuscripts in preparation:

Mantziara, M., Holland, P., Egan, C., Galea, J., & Kornysheva, K. (in preparation). Neural planning of sequences produced with different speeds.

Yewbrey, R., Mantziara, M., & Kornysheva, K. (in preparation). Neocortical control of movement order and timing during sequence planning and execution.

Chapter 1

Introduction

This Chapter aims to introduce the research context by briefly touching upon the historical emergence of the key concepts of order and timing that this thesis set out to investigate. The Chapter then reviews the relevant literature to shed light on the up-to-date knowledge on motor sequence representation with regard to the processing of serial order and timing. Specifically, the literature review first focuses on neural network studies of different theoretical backgrounds that have provided models for a parallel *vs* serial sequence representation and discusses behavioral data that support either computational account. The review then examines more closely neurophysiological evidence in support of a parallel account of sequence representation with a focus on motor sequence planning. Subsequently, the Chapter delves into the mechanisms of motor timing, motor planning and its relation to sequence performance. The Chapter, finally, outlines the aims and objectives of the undertaken constituent projects and defines the boundaries of the research questions.

1.1 Research Context

1.1.1 Early descriptions of motor sequence organization and the concepts of serial order and timing

Sequential behavior is a remarkable manifestation of how we interact with the world through movement. As a motor skill, this ability manifests in fundamental types of sequencing behavior that are inherent to human development such as tool use, speech production, and writing, or are part of artistic and athletic competence in the domains of dancing, musical performance, and sports.

The ability to smoothly execute a motor skill involves efficient assembly and coordination of muscle synergies for generating a sequence of actions in the correct order through time (Doyon et al., 2018). A number of neurological disorders, however, disrupt this function, heavily affecting the individual's ability to smoothly complete sequential tasks and activities in their everyday life. For example, children with Developmental Coordination Disorder (Sarmiento & Lau, 2020) exhibit significant difficulties in acquiring and performing motor skills due to poor learning strategies during training (Biotteau et al., 2016) and impaired motor planning (Bhoyroo et al., 2018, 2019; Krajenbrink et al., 2021). Similarly, stuttering, a speech disorder characterized by an interruption of timed and coordinated movements necessary for producing fluent speech (Ham, 1999) has been associated with motor speech planning deficits (Frick & James, 1965) as shown by behavioral (Walsh et al., 2015) and neuroimaging studies (S. Brown et al., 2005; Garnett et al., 2018). Defective planning and execution of motor sequences are also prominent in other motor speech sound disorders such as acquired apraxia (Duffy, 2005; Malcolm R., 2011; Bislick et al., 2017) and developmental verbal dyspraxia (Bradford & Dodd, 1994; Tükel et al., 2015) and extend to learning disabilities such as dysgraphia (Adi-Japha et al., 2007; Biotteau et al., 2019) which affects orthographic coding and finger order sequence planning in handwriting and typing (Raymer & Rothi, 2015). In addition, patients with cerebellar disease exhibit impaired control of timing severely affecting their ability to integrate visuomotor information and timely execute subsequent actions (Bares et al., 2007). Sequencing is also impacted in patients with Parkinson's disease (Ruitenberg et al., 2015) who show difficulty in planning complex sequential movements (Altgassen et al., 2007; Fritsche et al., 2020; Harrington & Haaland, 1991), impaired storage working memory (WM) capacity and incorrect retrieval of serial order (Witt, 2021; Ye et al., 2021). Collectively, this evidence points to an impaired interplay between the cognitive system and motor network responsible for controlling the optimal selection, planning, and execution of the intended sequential actions, impacting the orderly output of constituent movements over time.

Long before the above empirical observations came to light, understanding the underlying mechanisms of motor sequence organization, learning and control had been the centre of interest for early behavioral and cognitive scientists. The pure behaviorist view proposed a serial learning mechanism based on the *response chaining hypothesis* (Bain, 1864; James, 1891) and the classical conditioning laws (Watson, 1913; Watson & Rayner, 1920; Pavlov, 1927/2010). According to this account, sequences emerge when a stimulus (e.g., in form of proprioceptive feedback) paired with

a response triggers another response. Once this habitual connection is established, movements unfold smoothly in a serial manner with the stimuli paired with one movement element cueing the next. Ebbinghaus's (1885/2014) pioneering experiments on verbal serial learning and memory led to the formulation of the *associative chaining hypothesis*. His observations primarily supported the assumption that encoding of serial order information is possible due to strong associations made between adjacent items in a sequence. Thus, the mechanism for retrieving the serial order of a well-learnt list of items would involve a forward 'scan' of the chain of associations between the successive items. This hypothesis dominated for many decades providing a strong account of sequence control which generalized in the field of motor sequence learning.

However, the fundamental question pertaining to human cognition and motor control was fully encapsulated by Lashley K.S. in his thought-provoking essay on *The Problem of Serial Order in Behavior* (1951): How does the healthy brain achieve the integration of movement elements of familiar or well-learnt sequences into the desired order and how does that translate to a temporally structured sequence during execution? Drawing mainly on examples from the language domain, Lashley reduced the serial order problem to a need for understanding the generalized 'syntax' of serial movements. In rejection of the chaining theories and response-produced feedback dependent (i.e., closed-loop) control systems, Lashley introduced a hierarchical account of serial learning. His main criticism on the chaining account centered around the argument that an associative chain of movements cannot explain the flexibility seen in many motor skills. For instance, the innumerous combinations of phonemes to produce words in speech, or of notes to perform a musical piece cannot merely reflect pairwise linkages between successive elements. Instead, Lashley proposed that, for serial behavior to occur, a multi-level organization of plans is required which guides in a hierarchical fashion activity and output. In addition, Lashley was the first to challenge the role of sensory control arguing that it is unlikely that there is time for peripheral feedback to facilitate skilled, rapidly performed movements. Crucially, earlier empirical observations of intact motor control of limbs despite absent kinesthetic feedback (Lashley, 1917; Lashley & McCarthy, 1926; Lashley & Ball, 1929) set the basis for the hypothesis of a purely central motor program independent of peripheral feedback.

Lashley concluded that, in such centrally controlled system, action plans of the intended sequence are partially excited in parallel, namely preactivated simultaneously, before order is assigned to movements. In this structure, a timing mechanism, being at the time the most elusive to

explain, was speculated to interact with the spatial system (order) regulating the temporal structure of the sequence elements through some scanning process. Lashley's views on the spatial and temporal systems prescribe that the action plans or motor programs are already at play rendering the neural system dynamic before movement initiation. This critical thesis challenged the long-standing principle underlying the chaining mechanisms – essentially an axiom at the time held by physiologists - that the brain is static until the nervous system receives a stimulus of some form which triggers a chain of actions or reflexes. In addition, that action plans are encoded and 'readied' independently of muscular control and hierarchically organized introduced to motor neuroscience the seminal hypothesis that sequence representations may be modular in that different modules, i.e., sequence components (Keele et al., 2019) and/or neuromotor synergies (Poggio & Bizzi, 2004), interact to produce known or novel movements.

The rigid central – peripheral dichotomy argument received criticism from closed-loop theorists (Adams, 1971; R. A. Schmidt, 1975) while there was later consensus that the role of sensory feedback in skilled sequence control even for rapid movements cannot be precluded (Adams, 1976; Keele & Summers, 1976; Abbs & Winstein, 2019; MacKenzie & Van Eerd, 2019). Importantly, it has been suggested that an alternative account to chaining is not a strictly central non associative process (Bruce, 1994) as associations can take place under certain conditions in reaching movements (Desmurget & Grafton, 2000), naturalistic action sequences (Botvinick & Plaut, 2004), immediate serial recall (ISR) (Botvinick & Plaut, 2006; Chance & Kahana, 1997), simple structures in typing (Keele et al., 2003), episodic memory retrieval (Murdock, 1993), and repetitive movements (Yamashita & Tani, 2008). Despite these criticisms, the motor programming hypothesis has been widely accepted as the key notions of hierarchical organization and modular control of movement sequencing have fed or inspired several modern theories and models of sequence representation and control (Keele, 1968; Keele & Summers, 1976; Foster, 2002; Rhodes et al., 2004; Keele et al., 2019).

1.1.2 Contemporary computational approaches on motor sequence control: Basic architecture, principles, and assumptions

Understanding the mechanisms of sequence control has substantially benefited from the advancement of connectionist modelling especially over the last 50 years in the field of cognitive

science. Connectionism is a theory of information processing and refers to computational approaches for studying human cognition by using artificial neural networks. Without aiming at building direct analogues of biological neural networks, connectionist models focus on simulating the neurophysiological functioning of neurons and their networking in the brain by specifying their computational properties to explain the workings of cognitive phenomena (Houghton, 2005). Connectionist systems hypothesize that information is processed through connections among distributed representations. In an artificial neural network, these are in a form of highly inter-connected neuronal units, which represent patterns of neuronal activation rather than activation of individual neurons (Fodor & Pylyshyn, 1988; Medler, 1998; Walker, 1992; Zhang et al., 2020).

To date, the prominent connectionist models of sequence representation find their roots in early cognitive theories of serial learning. The first mathematical specification of Lashley's impactful motor program hypothesis (Lashley, 1951) was formulated by Grossberg (1978a, 1978b). His model on explaining short-term memory (STM) phenomena observed in free serial recall tasks is the computational ancestor of a class of neural networks accounting for a hierarchical organization of sequence learning and control, termed competitive queuing (CQ) models (Houghton, 1990). Expanding on the theoretical concept of simultaneous plan representations, Grossberg provided the basis for the two fundamental assumptions that all CQ networks follow in a system consisting of two primary neural levels or layers (Bullock & Rhodes, 2003; B. J. Rhodes et al., 2004): First, multiple plan representations (nodes) can be concurrently active in a layer called parallel planning layer, and second, in a competitive choice layer those plans compete with one another until the most active plan is selected for output (Figure 1.1).

During sequence retrieval, the co-activated plans (i.e., sequence elements) are accessed in a neuronal map in a parallel planning layer, featuring a *primacy gradient* (Grossberg, 1978a, 1978b; Page & Norris, 1998), which reflects graded neuronal activation levels across plans. In the competitive choice layer, plans are controlled by *recurrent competitive field* (RCF) dynamics, part of the WM system, which normalize total activation across the competing plans (Grossberg, 1978a). One significant property of this normalization is that the distributed activation patterns are preserved in the planning layer via recurrent self-excitation of the most active plan and inhibition of all competitor plans. Whilst excitatory activity is thought to reflect the co-firing of excitatory neuronal populations, lateral inhibition is modulated by interneurons. Lateral inhibition is a well-established mechanism of neuronal specification which allows neurons to focus their activation by

suppressing the firing of surrounding neurons and increasing signal-to-noise when a consistently strong signal is received (Sillito et al., 1985; Kral & Majernik, 1996; Appel et al., 2001; Sil'kis, 2006; Beck & Hallett, 2011; Bakshi & Ghosh, 2017; Sugawara, 2020). In the CQ system, lateral inhibition allows the plan with the strongest activation to be chosen through a 'winner-take-all' mechanism, a second property of the RCF normalization. Once the selected plan wins the competition and is selected for execution, it is 'deleted' from the parallel planning layer, reflecting its suppressed activation (inhibition). Due to the RCF dynamics, after a plan is deleted, activity is redistributed across the remaining plans still maintaining the rank ordering of the initial activation levels. This activity preservation in the planning layer has as a consequence the activation level per plan to be reduced as a function of the number of simultaneous plans. Finally, all parallel plans are effectively converted to serial production over time through this iterative process terminated by the last plan of the sequence being selected for execution.

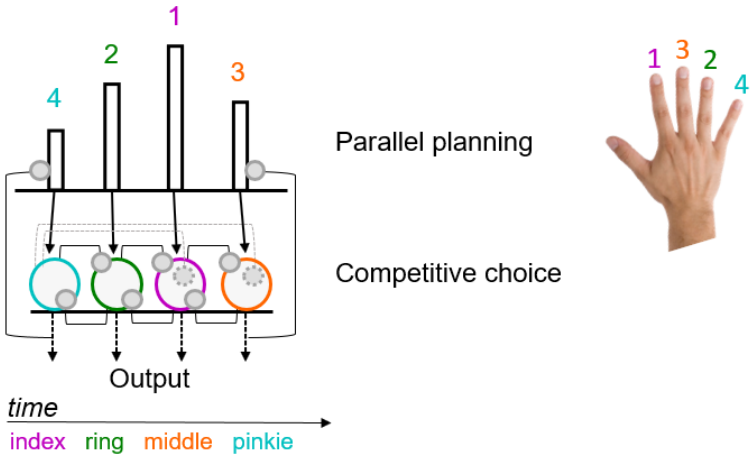


Figure 1.1 | CQ network. The operation of a CQ network is described here in the context of motor sequence control using a hand model for a four-element finger sequence. The parallel planning layer comprises a high-level map containing the plan representations of movement elements that constitute the learned or encoded sequence. The plans are simultaneously activated with their activation strength depending on their position in the sequence. Once the sequence is retrieved, the most active element (i.e., 1st) is self-excited (solid arrow) and at the lower-level layer (competitive choice) competes with each of the neighboring nodes by sending inhibitory signals (brackets with gray circles, solid and dashed versions). To avoid clutter, inhibitory connections with all other nodes (dashed version) are exemplified only for the node corresponding to the 4th element. When the most active element wins the competition, it is executed (dashed arrow) and then self-suppressed from the parallel planning layer (depicted with sided brackets with gray circles). Every next most active element (2nd, 3rd…) undergoes the same stages until the motor sequence is produced and the parallel planning layer is blank. Following this cyclic iterative process, the CQ mechanism allows for a forward conversion of the parallel plans to serial output over time. CQ, competitive queuing. Adapted from Bullock and Rhodes (2003).

In a parallel strand of research, the 'connectionist revolution' in the 1980s popularized the use of recurrent neural network (RNN) models due to significant advances in their functionality and applications (Rumelhart et al., 1986). Inspired by the architecture of biological neural networks, RNNs have been developed from their basic form (Hopfield, 1982; Elman, 1990; Jordan, 1997) to more sophisticated algorithms (Bianchi et al., 2017; Wang et al., 2017; Caterini & Chang, 2018) and have become very powerful in explaining a wide range of time series or sequential data (Kanagachidambaresan et al., 2021). Originating from the classic associative chaining hypothesis (Ebbinghaus, 1885/2014; Washburn, 1916/2008), recurrent neural systems posit that a practiced – either discrete or continuous - sequential behavior is fundamentally represented serially, yet as a cohesive system. Specifically, their architecture is based on the principle that, during sequence learning, serial movements are encoded as a chain of associations between the successive elements that comprise the learnt sequence. The primary assumption is that for the sequence elements to be generated in the intended order, each element in the chain cues and retrieves the one that successes it. This property of dependency, in turn, subserves the assumption that no feature of the sequence is preprogrammed, namely there is no 'pre-registered' element-specific information in place. Instead, any current element's information is both dependent on the previous element's information and time-dependent as it is successively elicited while the sequence elements are serially executed.

Technically, in an RNN application, generation of a spatiotemporal trajectory of a trained sequence is controlled through feed-forward and feed-back – hence, recurrent – signals. In a network consisting of an input, a hidden, and an output layer, each output sequence element is fed back to the hidden layer as input. Through this feed-back loop, the hidden layer - a node preserving sequential memory information - is fed by a context-specific, e.g., spatiotemporal, state both of every current and previous input before the output element is determined (Sherstinsky, 2020; Ashraf Zargar, 2021). In modelling sequence representation at the neural level, this means that the state of an output neuronal population activity at a specific time, y_t, defines the order and timing representations that feed the current input activity state and triggers the next output neuronal population activity y_{t+1}. This, in turn, triggers activity y_{t+2} and so on, until the whole sequence is generated (Figure 1.2). Therefore, the spatial order of an element within a sequence (i.e., its ordinal position) can only be represented serially as it is intrinsically dependent to the occurrence of the previous data. Elman (1990) has proposed that time in an RNN system can be stored as an internal

representation, thus implicitly, by utilizing an error signal in the form of feedback to guide the temporal structure of the sequential elements.

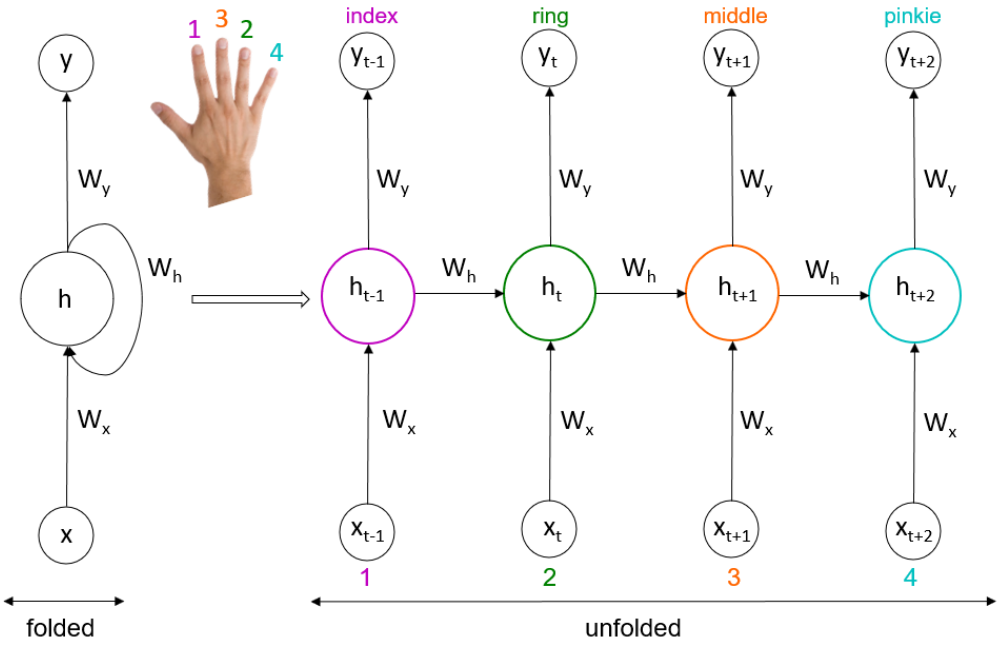


Figure 1.2 | RNN in folded and unfolded states. An RNN consists of three distinct layers, the input (x), hidden (h), and output (y) layers, each of which is assigned with different weights (w_x, w_h, w_y) serving to facilitate the network's ability to learn. Similar to the CQ illustration (Figure 1.1), a hand model for a four-element finger sequence is used as an example of motor sequence control. Here, an element representation (e.g., 1st, as starting point of the finger sequence) is fed to the input layer (x_{t-1}) whose information is sent to the hidden layer (h_{t-1}). The hidden layer maintains the sequential memory. Once the current element is output (y_{t-1}), the information in the current hidden layer (h_{t-1}) is passed over to the next hidden layer (h_t) so that the system 'knows' element 1 has been output. The process is serially repeated (hence the multiple 'single' RNNs as shown in the unfolded version) until the motor sequence is completed. RNN, recurrent neural network. Adapted from Ashraf Zargar (2021).

1.2 Literature Review

1.2.1 A parallel *vs* serial sequence representation of order and timing

A sequential motor skill is characterized by our ability to proficiently conduct deliberate and goal-directed series of movements. Motor sequence acquisition involves the learning of novel patterns through practice to ensure a gradually more efficient, i.e., faster and more accurate, execution of the intended sequential actions (Shmuelof et al., 2012; Whiting, 1975; Willingham, 1998). How the brain accomplishes the organization of distinct movement elements into sequence outputs in the correct order and in a timely manner remains debatable.

1.2.1.1 Neural network studies of sequence representation and relevant behavioral data

A significant proportion of the literature on sequence representation is assigned to neural network studies. As previously mentioned, these typically represent two different schools of thought, namely a parallel versus serial processing account of sequence learning and control. Variants of CQ models have been developed to simulate a wide range of serial performance data. These include action selection (Cooper & Shallice, 2000), verbal, spatial and visual serial recall from STM (Gupta & MacWhinney, 1997; Hurlstone & Hitch, 2015, 2018; Henson, 1998; Page & Norris, 1998; Burgess & Hitch, 1999; Glasspool, 2014), speech and language production (Bohland et al., 2010; Glasspool & Houghton, 2005; Grossberg, 1987; Hartley & Houghton, 1996; Hitch et al., 2022; Houghton, 1990; J. Ward et al., 1999), and typing and handwriting (Bullock, 2004b; Bullock et al., 1993; Rumelhart & Norman, 1982). Mathematical models based on CQ principles have also expanded from saccadic eye movements (Grossberg & Kuperstein, 1986), planning and production of sentence and musical sequences (Page, 2019; Palmer & Pfordresher, 2003; Pfordresher et al., 2007), to storage of arbitrary sequential events (Bradski et al., 1994) or one-shot learning of novel behaviors (Jändel, 2014).

The application of CQ models to a large variety of serial behavior domains demonstrates that a CQ network may describe a central mechanism of sequence learning, planning and control (Houghton, 2005; B. J. Rhodes et al., 2004). On the other hand, RNN models have been used to explain specific human cognition functions and motor behaviors such as associative memory (Lewandowsky & Murdock, 1989; Murdock, 1982, 1983, 1993), and sequential neuronal population activity underlying rhythmic movements or stereotyped actions (e.g., Bruno et al., 2017; Cannon et al., 2015; Kleinfeld & Sompolinsky, 1988). Thus, although the present research focuses on motor sequence representation, in this review modelling studies are discussed with regard to how they suggest serial order and timing are encoded in order to plan and generate sequences in various domains (motor, speech, etc.), as the principles are common across serial behaviors. Importantly, studies modelling sequences from STM are discussed first since they provide the basis in variants of CQ or RNN models for also modelling sequence representation and retrieval from long-term memory (LTM). Additionally, this review covers the models' predictions for serial order phenomena observed in human behavior (e.g., reaction times, errors), and their relevance to behavioral findings.

1.2.1.1.1 Short-term memory

The CQ structure of parallel representation is very different from an RNN architecture where there lie direct pairwise associations between successive items comprising a sequence; these direct links are thought as key in associative sequence encoding during learning, as well as in planning and execution. A CQ architecture, on the other hand, can be very specific as to how serial order of planned actions is represented in the planning layer where multiple candidate plan representations are simultaneously active. Various types of CQ modelling specify differently order encoding. In the CQ planning layer of *ordinal* models, the primacy gradient comprises the most basic functional mechanism assuming one-dimensional ordinal encoding. The gradient is established during sequence learning over the constituent plans such that activation levels monotonically decrease across positions. For example, as originally shown by Grossberg (1978b), when recalling a list of items from STM, items presented earlier in the sequence were assigned stronger activations than later items. Several models of ISR (Farrell & Lewandowsky, 2002, 2004; Grossberg & Pearson, 2008; Page & Norris, 1998) support encoding of serial order information based on the activation level (or otherwise strength) whereby a primacy gradient is formed depending on the items' initially presented order.

However, characteristic of the activation gradient in ordinal CQ models is that it remains static as sequence production unfolds making them inadequate in simulating order errors in sequence retrieval (Burgess & Hitch, 2005). In that front, the primacy model of Page and Norris (1998) has made a significant contribution proposing time-decaying activations of constituent item representations which though are susceptible to noise when the primacy gradient is formed. Specifically, the authors predicted that each constituent item's activation during planning increased more with every other item presented or experienced during encoding and attenuated as a function of time during retrieval, selection, and output. Order errors in retrieval could emerge because an item may incorrectly acquire stronger activation than its preceding item due to random noise in input encoding thus causing transposition errors in adjacent items. Criticism, however, persisted regarding the capacity of ordinal models to predict a wider range of error patterns reflecting positional confusions, such as protrusion errors[1] on a trial-by-trial basis (Henson, 1998b; Nevill et al., 1996; Burgess & Hitch, 1999).

[1] Protrusion errors refer to incorrectly recalling an item in sequence *n* at the same position as in sequence *n-1* (Conrad, 1960; Henson, 1998b; Ryan, 1969).

Houghton (1990) proposed a more flexible mechanism by suggesting that what controls serial order of selected plans during production is a rather dynamic gradient which determines the rank reordering of plans in the parallel planning layer by modulating their activation and controlling their production through time. This has been also described as an emergent gradient which determines on the fly the activation level of phonemic elements, before the production of the intended word, based on additional input (e.g., semantic and/or syntactic) which updates the system (Ward, 1994). The operation of such activation dynamics renders the network more effective for explaining non-adjacent items errors especially seen in speech production (Rhodes et al., 2004). In Houghton's CQ algorithm for learning and producing phonemic sequences (i.e., words), apart from the initial (primacy) gradient acquired during learning, a graded activation pattern over the planned sequence elements (phonemes) is preserved through sequence generation. All elements' activations gradually increase until the most activated element is selected for output and then suppressed. Both the decreases in activation of neighbouring elements due to the lateral inhibition from the winner and the gradual increase (rebound) of the next most activated element yield relative activations which govern through time the order in which each element becomes the winning response. Because each element is temporally constrained by start and end edges (see also Henson, 1998b), the sequencing mechanism of graded activations controls at the same time the temporal order of winning responses making the use of explicit position-specific information redundant. This model was the first most comprehensive computational expression of non-associative links postulating a hierarchical control of sequence learning and control. However, it did not clearly address the occurrence of protrusion errors. Another criticism it has received regards the automatic inhibition of the selected action. This is applicable only to units at the lower level of the hierarchical structure, thus units at higher levels either preserve their activation until the action or aspect of the sequence they represent is executed (Cooper & Shallice, 2000), or separate mechanisms should control their activation/inhibition (Botvinick & Plaut, 2004).

More advanced CQ models of STM have taken the idea of the dynamic gradient a step further by employing a position marking mechanism in conjunction with the primacy gradient for representing serial order (Brown et al., 2000, 2007; Burgess & Hitch, 1992, 1999; Henson, 1998a, 1998b, 1999; Hurlstone & Hitch, 2015, 2018; Lewandowsky & Farrell, 2008). Such *positional* models were inspired by the crude principle that serial order is controlled by means of ordinal position 'slots' that each sequence element occupies or is assigned to (Conrad, 1965). In practice,

however, such a hardcoded mechanism of item-position associations can evoke significant noise in the system during recall of a sequence collapsing its correct performance. To account for sequence disruption because of order errors, early models (Estes, 1972; C. L. Lee & Estes, 1977, 1981) used the positional information as a context signal which changes as a function of time assuming direct item-position associations. Here, order errors occurred due to perturbations of the timings of item-position associations causing reordering of the reactivation of items. Further, Burgess & Hitch (1992) demonstrated that recalling items in the correct order in an ISR task by accessing the corresponding positional tags was highly imprecise introducing transposition (order) errors because of overlapping representations of neighbouring positions. As mentioned above, Page and Norris (1998) attribute this persistent error pattern to a 'fill-in' phenomenon during which an item is recalled at an earlier position (e.g., 1st) in the sequence than it should, so the next position (2nd) is filled in by the item that should have originally been recalled at that 1st position. Empirical evidence (Farrell et al., 2013; Surprenant et al., 2005) also support this finding contradicting chaining models which hold that once an item 'hijacks' an earlier position, it would cue the item that succeeded it during encoding.

Burgess and Hitch (1999) in their powerful context-based positional CQ model of the phonological loop introduced a context signal for encoding position as an additional dimension in the network. Simply put, the activation (primacy) gradient over plans of sequence item representations dynamically changes over time receiving input from another layer, that of ordinal position context signal, throughout sequence production. In their model, when an item is retrieved as part of a to-be-performed sequence it is activated in the parallel planning layer. Via Hebbian learning (Attneave & Hebb, 1950; Hebb, 1961; also *cf*. Hebb repetition effect; Couture & Tremblay, 2006; Cumming et al., 2003) the item-position association is formed. Expanding on Houghton's (1990) work on an intrinsic temporal organization of within-sequence items, key in these item-position associations is that the positional context information is a time-varying signal that resets after the end of a sequence and at the start of recalling the next sequence. To successfully recall the sequence, the system updates the positional context via rerunning the timing signal such that an item representation is associated with the current state of the positional context signal. This establishes a dynamic activation gradient over the items which varies over the generation of sequence elements one-by-one through time and allows the retrieval of the most activated item at its corresponding position as embedded during learning. In the regime of modelling STM of verbal or even non-

verbal sequences (Smyth et al., 2005) it has been postulated (Burgess & Hitch, 2005) that the positional information is accessed through the episodic buffer in the context of Baddeley's model of WM (Baddeley, 2000).

The timing signal component either as a moving temporal context (Burgess & Hitch, 1999, 2006) or oscillatory (Brown et al., 2000, 2007; Hartley et al., 2016) signal makes an important contribution to our understanding of a potential role of sequence timing, or else temporal structure, in item representation depending on positional information. In these time-based CQ models, the timing signal is a moving window or an oscillator operating at varying frequencies that regulates the current positional state of an item and renders adjacent activation states of the positional context signal more similar than states that are more distant in time. Therefore, here, temporal information of sequential items interacts with the positional information indicating their occurrence during encoding and recall. Simulations of the time-based CQ models have focused on addressing the explanation of temporal grouping effects during sequence production first demonstrated experimentally by Ryan (1969). Using an auditory task of ISR of nine-element sequences, Ryan showed that temporal grouping (i.e., dividing a long sequence into shorter groups by introducing distinct pauses in between) of sequential items affected the shape of the acquired accuracy serial position curves[2] and the pattern of errors. Specifically, not only were there within-group primacy and recency effects (Jahnke, 1965), but importantly within-group order errors were reduced. However, items still tended to preserve their position in neighbouring recalled groups (i.e., between-groups transposition errors) implying the existence of between-groups representations of positional information. The above time-based CQ models successfully predicted an increase in probability to recall an item at its correct - or an adjacent to it - position when items are temporally grouped than when they are presented in longer sequences with isochronous inter-item intervals. In addition, consistent with Ryan's findings, these models could predict an increase of between-groups positional confusions accounted for by between-groups representations, where items belonging to different groups transpose to the same position. Unlike the predictions of chaining-like

[2]In the literature of serial order, a traditional approach to illustrate sequence production data is by plotting separately the correct percent and reaction time of correct trials as a function of the sequence elements upon recall by their serial position. These data are visualized as accuracy and latency serial position curves, respectively, both describing the profile of sequence production. The accuracy curves exhibit a U-shape curve with pronounced primacy and recency effects (Deese & Kaufman, 1957; Jahnke, 1965; Murdock, 1962; Robinson & Brown, 1926) indicating the recall accuracy of each serial position. The latency curves typically form an inverted U-shape profile whereby RTs reflect the time required for each element to be output.

models, these computations also corroborate a hierarchical representation of serial order where positional information of items and sequences (groups) is encoded simultaneously but quite independently.

While on the CQ modelling front, substantial developments have been done to predict various patterns of errors, chaining models have been heavily criticized on their limitation to simulate behavioral benchmarks in serial order recall (Hitch et al., 2022). Although the chaining hypothesis was long thought to provide a relatively valid account for STM of serial order (Lewandowsky & Murdock, 1989; Wickelgren, 1966), pure forward inter-item associations have been inadequate to explain simple or complex patterns of errors (Botvinick & Plaut, 2006; Burgess & Hitch, 2005; Houghton & Hartley, 1995; B. J. Rhodes et al., 2004; Rosenbaum, 2010). Baddeley's (1968) data on acoustic similarity effects on serial recall were the first to empirically refute a chaining account. While participants were instructed to recall sequences of alternating phonemically similar and dissimilar items (here, consonants), critically it was found that they were able to produce the mixed sequences as accurately – namely, retrieving the items in their correct position - as the sequences made of entirely dissimilar items. This empirical finding disproves the prediction followed by a chaining mechanism that, for instance, two dissimilar items cannot be recalled in their correct position if they are cued (i.e., preceded) by similar items, thus causing confusion in serial encoding, planning and production (see also Henson et al., 1996).

In addition, associative intrusion errors of adjacent dyads erroneously being recalled in new positions - still though preserving their adjacency – are predicted by simple chaining models to occur pretty often (Wickelgren, 1966) due to the rigid inter-item associations. However, behavioral data by Henson et al. (1996) demonstrated that such errors are much less frequent. Further, simple chaining models could not predict transposition errors where an item exchanges positions with adjacent items, as that item would just 'activate' its following one - certainly not the replaced item. A more advanced class of chaining models, using compound chaining mechanisms (Murdock, 1995; Solway et al., 2012), have overcome the problem of such simple within-sequence order errors by using bidirectional (forward and backward) and graded inter-item associations. However, more complex error patterns such as omissions and protrusion errors remain unaddressed by RNN, i.e., chaining-like, models since these would predict premature termination of sequence retrieval and production.

Botvinick and Plaut (2004, 2006), while agreeing that simple chaining cannot explain complex sequencing behavior and sequence performance effects, have proposed that a more sophisticated RNN architecture holds promise for an account of action selection in routine naturalistic action sequences or serial recall from STM. Botvinick and Plaut (2006) demonstrated that by using extensive training and back-propagation (Rumelhart et al., 1986) they were able to simulate Baddeley's (1968) findings. Their model exhibited similarity to a CQ hierarchical-like structure in that sequence elements were superposition-coded: Each element was represented with a unique activation pattern and the whole sequence was represented as a summation of those patterns in the hidden layer. Although elements were represented independently based on their ordinal position, item identity and positional information were represented together such that an item's representation changed depending on its within sequence position. Contrary to the CQ model of Cooper and Shallice (2000), the same group (Botvinick & Plaut, 2004) simulating a naturalistic task, reproduced omission errors as observed in apraxia patients with acquired brain injury (Schwartz et al., 1991, 1998). However, both RNN models could not fully capture other sequence performance effects like protrusion errors or grouping effects. These models oppose by virtue a traditional hierarchical account for sequence representation in motor control as proposed by early theorists (Lashley, 1951; Miller et al., 2017; Restle, 1970). In a holistic hierarchical structure, as the CQ models employ, separate representations are assumed for flexible control of aspects of the sequential action.

Interestingly, Botvinick and Plaut (2004) successfully simulated a naturalistic serial behavior with an RNN model. They adopted a quasi-hierarchical structure in line with the task's nature where different main tasks (e.g., making coffee) consist of several sub-actions (e.g., grab the cap, add sugar, and so on), handled at higher and lower levels of the network. This RNN system employed multiple internal representations qualifying it as quasi-hierarchical; these were 'indexical' representations in the hidden layer of the network reflecting the possible target actions, and were not preactivated, instead they evolved with experience as the sequence unfolded over time. One limitation in this simulation is that the model assumes that action selection and object selection involve common processes in that object-directed actions are perceptually selected and guide the action. Empirical data from fronto-parietal patients and healthy participants indicate that functional relations between objects (e.g., mug, coffee, kettle) affect perception such that when spatially close together they create an attentional bias for grouping these related objects into a unified action

representation improving performance (McNair & Harris, 2014; Riddoch et al., 2003; Wulff & Humphreys, 2013; Yoon et al., 2010). Thus, it is unclear what defines the changing of attentional focus over the different objects, as postulated in the input representation layer of the Botvinick and Plaut's (2004) model. In addition, the intermingled representations of action and object selection assumed here contradict behavioral findings (Boutsen & Humphreys, 2003; Riddoch et al., 2000) which show a dissociation between object selection and action (i.e., effector) selection. Here, patients with cortico-basal degeneration or damages to temporal and medial-frontal cortices had a deficit in selecting the correct effector but no impairment in selecting the correct object, suggesting that these processes are most likely represented independently. Also, the quasi-hierarchical account (Botvinick & Plaut, 2004) appears to make a prediction of a flexible overlapping representation of effectors, chunks, and sequences. Functional neuroimaging (fMRI) recordings, however, provide a clear dissociation in the primary motor cortex (M1) area which appears to encode only the individual movements constituting the learnt sequences and not the sequence itself (Yokoi et al., 2018). On the other hand, the same group (Yokoi & Diedrichsen, 2019) found that chunks and sequence representations overlap in the premotor and parietal cortices. This favors a partly quasi-hierarchical account which posits that different encodings can be accommodated in one level of representation.

The assumption of the CQ framework, following the motor programming theory, that constituent plan representations of a sequence are simultaneously active, implies that movements are preactivated and planned in advance of movement initiation. This is a prediction not met by RNN models. Behaviorally, the hypothesis that a movement is prepared before it is executed was directly tested by Henry and Rogers (1960) in their memory drum hypothesis. Using movement tasks of varying demands, they found that reaction time (RT; interval from a ‘go’ signal to movement onset) increased with movement complexity (e.g., increased demands and sequence length). The assumption here was that RT reflected the time needed to prepare the movements as determined by their complexity and attributable to slower access to the stored patterns of movement representations. Sternberg et al. (1978) reported a similar effect focusing on sequence length and execution rate based on the produced inter-response-intervals of constituent items. In typing and speech tasks where participants recalled sequence lists of different lengths after a short practice, both RT of the first item and mean inter-response-intervals were found to linearly increase with the length of the retrieved sequence. In addition, the inter-response-intervals of constituent items were dependent

on their serial position in the retrieved sequence. These data were explained within a more refined sequence preparation hypothesis of motor programming that sub-programs, being the constituent plan representations of a motor program of a sequence, are encoded and after a trigger they are prepared by being assembled and loaded into a motor buffer.

The above effects have been investigated for establishing behavioral markers of motor planning in neurological patients exhibiting delayed sequence initiation or timing deficits during execution. Studies have shown that although patients with Parkinson's disease typically produced sequences with increased inter-response intervals and longer execution times than healthy controls, they showed no difference with regard to sequence length and serial position effects (Agostino et al., 1992; Rafal et al., 1987; Reilly & Spencer, 2013). These behavioral findings suggest that patients with disrupted cortico-basal ganglia-cerebellar network have an intact ability to learn short sequences and retrieve prepared sequential movements in advance of sequence execution (as opposed to longer sequences; e.g., see Harrington & Haaland, 1991; Smiley-Oyen et al., 2007) albeit with impaired control of interval timing. This is in line with neurophysiological evidence showing that activation in the basal ganglia (BG) and the cerebellum during motor planning accounts for controlling movement initiation and interval timing (Kunimatsu et al., 2018). At the same time, the preservation of the temporal order of intended movements may be spared by the prefrontal cortex, allowing for the correct retrieval and planning of movements (Beiser & Houk, 1998) via corticostriatal loops (Alexander et al., 1986).

The replicable effect of sequence length on RT (e.g., Kilbourn-Ceron & Goldrick, 2021; Magnuson et al., 2008; Van Lieshout et al., 1996; Wright et al., 2009) directly refers to the CQ network operation. The CQ principles follow the prediction that the time to perform the first planned item increases with the plans concurrently active in the planning layer due to the normalization of activation levels relative to their number (Bullock & Rhodes, 2003). Notably, Boardman and Bullock (1992) developed a two-layer CQ network in which the time required for a planned item to be selected as the winner movement depends on the strength of the activation level of its respective input representation. This model reproduced Sternberg et al.'s (1978) critical findings by predicting not only the effect of sequence initiation and interval timings of the remaining output sequential movements on RT but also the interval timing changes as a function of serial position. Further, Farrell and Lewandowsky (2004) successfully simulated the serial position effect on RT

latency by producing the characteristic inverted U-shaped serial position curves. In the CQ environment of all positional models such an effect is reproducible because plans in the sequence boundaries (i.e., first and last positions) have more distinct positions markers than the in-between plans facing, as a consequence, less competition from neighbor plans during recall.

1.2.1.1.2 Long-term memory

Beyond the parallel processing of sequential movements recalled from STM, CQ modelling also possesses an advantage of simulating sequences interfacing with LTM. As opposed to Sternberg et al.'s (1978) task, when sequences are extensively trained the effect of sequence length on RT is extinguished (Klapp, 1995; Verwey, 1999; D. L. Wright et al., 2004). This phenomenon has been attributed to the integration of sequence elements into chunks with more practice, permitting faster programming, hence, in turn, faster initiation, of the retrieved sequence (Klapp, 1995). Rhodes and Bullock (2002) developed a cerebellum-based CQ model successfully simulating the above behavioral data. The authors' model was based on a fast recall process of over-learnt discrete movement sequences where different sequence chunks are rapidly loaded in parallel from LTM to WM. Specifically, the cerebellum, as part of LTM, builds activation gradients of 'compressed' sequences during sequence learning and 'expands' them into the WM buffer, i.e., the planning layer consisting of the constituent normalized plans (Rhodes et al., 2004). Strong learning enables the pre-selection of a sequence based on its first element invoking a substantial reduction to the time required to recall the sequence.

By contrast, traditional RNN models have an intrinsic problem in simulating LTM storage and retrieval or even very long sequences due to their restricted capacity to go back in time only a few timesteps (Mozer et al., 1992). Advances in deep learning, however, have given rise to a new variant of RNN, the Long Short Term Memory (LSTM) RNN model (Schmidhuber, 2015) thereby solving the problem of capturing long-term dependencies in time. By training a continuous-time RNN to learn long-term dependencies, Laje and Buonomano (2013) have modelled chaotic neuronal firing rate to generate spatiotemporal motor trajectories with a network that accurately encoded time. Additionally, a study modelled a complex sensorimotor task where spoken elements (sensory input) were encoded in high-dimensional state space (Goudar & Buonomano, 2018). The final motor output of respective transcribed elements was determined by transforming the high-dimensional trajectories to low-dimensional motor patterns by utilizing three coordinates of motor

output activity to finally generate a 3D written motor pattern. Importantly, this model was trained to store stable neural trajectories that were time-varying patterns such that to recognize and predict temporally warped output patterns. In both cases, this sequence modelling was possible due to specific parameters, such as the implementation of gated trajectories and innate training, which maximized the models' stability and accuracy. Focusing mainly on the control of timing, another study sought to address whether sequential responses produced from LTM are timed continuously or 'restarted' at each response (Laje et al., 2011). The behavioral results showed that both well-trained spatiotemporal (multi-finger) sequences and purely temporal (single-finger) sequences used a continuous timing strategy. The authors built a population-clock RNN model that could be trained in the target patterns of discrete movements and generate smooth spatiotemporal sequences consistent with the empirical data. In these models, order of a motor sequence is tantamount to time which, contrary to the CQ timing signal, is controlled by chains of neurons in a population operating in associative connections. Beyond the domain of motor control, Palangi et al. (2016) constructed a language processing RNN system with LSTM architecture which makes storage of sentence sequences to LTM possible by extracting and retaining semantic information. Still, extraction of semantics of each word in a sequence ('sequence embedding') was done in a serial manner adopting associative relationships between words in the hidden layer of the network. Simulations involved backtracking semantic representations during recall. However, they ignored the processing of precise timing through utilization of additional timing information (Gers & Schmidhuber, 2000) which would have allowed for temporal distinction between sequence elements. In addition, the latter computations do not have correspondence to empirical data thus providing at present a relative weak account of LTM sequence representation and recall.

1.2.1.2 Parallel planning of sequential movements: Neurophysiological findings

The CQ and chaining computational theories make opposing predictions as to the neurophysiological mechanisms of serial order representation. The cardinal antithesis of parallel *vs* serial processing of sequential elements follows at the neural level as well. The chaining theory predicts that sequence-related neural activation during execution is *sequential*, with all elements being activated one by one, i.e., at different time points. Although, chaining-compatible accounts do not pose explicit predictions about sequence planning, the process itself of each element becoming available/activated after the previous one is executed indicates that such seriality is assumed to

operate also during planning. By contrast, the CQ framework postulates *simultaneous* neural pre-activation of all constituent elements before movement begins, allowing for serial execution over time through the CQ iterative process.

Neurophysiological data from single-cell and multi-unit recordings from the non-human primate brain provide a rich pool of converging evidence on frontal lobe neuronal selectivity to the serial order of sequential elements. Usually, in these studies, the term serial order is used interchangeably with 'rank order' or 'temporal order' as in most cases activity has been identified in relation to *when* a movement occurred or was expected to occur relative to the other movements in a sequence (1st, 2nd, 3rd position and so on). Order-related neuronal activity in the frontal lobe area, especially the prefrontal cortex and supplementary motor area (SMA), has been at the centre of interest because of its role in various aspects of motor control (Nachev et al., 2008), from action monitoring (Bonini et al., 2014) to time perception (Protopapa et al., 2019), and in WM (Funahashi, 2017; Kimberg et al., 1997; Lara & Wallis, 2015). Together with impairment in temporal lobe structures (Hannesson, Howland, et al., 2004; Heuer & Bachevalier, 2013) and the BG (Rothwell et al., 2015; Yin, 2010, 2014), frontal lobe lesions are accountable for disrupting memory for serial order and the ability to form orderly sequences in humans (Beldarrain et al., 1999; Eslinger & Grattan, 1994; Luria & Tsvetkova, 1964) and animals (Hannesson, Vacca, et al., 2004; Petrides, 1991).

Specifically, the role of SMA and pre-SMA neuronal activity has been highlighted in the planning and control of temporal order of sequential movements in the seminal push-pull-turn experiments of the Tanji group. While a group of SMA neurons recorded in monkeys were selectively responsive, before movement onset, to a particular order of forthcoming movements, a different group in the same region was activated during sequence performance after the production of a specific movement and before the production of another one (Tanji & Shima, 1994). Interestingly, a dedicated neuronal population in the pre-SMA was consistently transiently activated at the moment where the monkey had to update the motor plans of the subsequent required sequence (Shima et al., 1996). In addition, the pre-SMA was found to increase activity during intervals between specific movements or before any of the serial positions regardless of the movement itself or the sequence (Shima & Tanji, 2000).

Directly probing ordinal position representation in these areas, another study recorded brain activity while monkeys had to produce three-element movement sequences at different starting points, directions and endpoints (Clower & Alexander, 1998). Here, a larger amount of pre-SMA delay and execution activity and less SMA delay activity reflected the ordinal position of a movement regardless of which movement preceded or succeeded it, suggesting a preference of pre-SMA in representing the ordinal position of sequential movements. Barone and Joseph (1989) tested monkeys in a visuospatial oculomotor task in which the animals had to identify by memory the correct order of three targets after a short delay. A type of neurons in the peri-arcuate oculomotor region of the prefrontal cortex exhibited sustained temporal selective activity: Different cells fired preferentially depending on which serial position a movement was associated with, whilst activity attenuated when the monkey performed the sequence in an incorrect order. In similar paradigms, the prefrontal cortex has shown serial order selective activity during the delay period where the monkey prepared the movements. Specifically, lateral prefrontal cellular activity was found to respond differentially to sequences consisting of the same movements but in different order (Ninokura et al., 2003) or to the rank order of a response alone or its rank order and the target's properties together (Ninokura et al., 2004). A different experimental manipulation led Funahashi et al. (1997) to dissociate prefrontal neurons that retain spatial positions (ordinal positions associated with specific locations) from neurons than retain both spatial positions and temporal order of their presentation. The latter neurons showed distinct pair-dependent and temporal order-dependent activity during the delay period. In addition, Berdyyeva and Olson (2010) demonstrated that neuronal selectivity to the ordinal position (rank order) of a target is widespread across different areas in the prefrontal cortex, i.e., the SMA, pre-SMA, supplementary eye field (SEF), and dorsolateral prefrontal cortex (DLPFC). Despite small variations, each area showed rank order activation during the retrieval (delay) and the execution periods of two serial order action and object tasks.

However, the above studies have focused on selective activity during serial order retrieval or execution without directly investigating neurons that encode the serial order information itself. While the human mid-DLPFC is implicated in short sequence encoding in WM (Amiez & Petrides, 2007), the monkey primary motor, premotor, and prefrontal areas were found to encode in concert the serial position of stimuli in sequences of different lengths (Carpenter et al., 2018). Consistent with behavioral findings from humans by Henson (1999b), these regions encoded serial position

in relative terms, namely depending on where in the sequence a movement occurs, rather than based on its absolute numerical position. Further, the question of whether there is a dedicated neural representation for preparing the system, after recall, to execute a sequence was addressed by Ohbayashi et al. (2003). The authors trained the animals to memorize a sequence and then direct their saccades to the locations of the recalled positions in forward and backward order. An order-dependent transient spiking activity in the monkey dorsal premotor cortex (PMd) (human homologue being the pars opercularis/ventral premotor cortex; Ferri et al., 2015; Rizzolatti et al., 2002) was elicited only after retrieval and before execution. This indicates that this area has a special role in encoding the conversion of serial order information stored in WM to a motor program by setting the motor system ready for executing the planned movement.

All together, these findings indicate that the frontal lobe has a key role in sequencing by maintaining the serial order of intended acts. Importantly, they indirectly refer to how context-based positional CQ networks (e.g., Burgess & Hitch, 1999, 2006) model the encoding and retrieval of a sequence and serial position information. Specifically, the above presented neurophysiological data collectively agree on the existence of separate sequence-specific or serial position-specific representations supporting or participating in the encoding, retrieval, or execution of sequences, depending on the demands and manipulations of the task. This rather reflects a hierarchical structure of representations operating in the brain, an axiom of the CQ class of models but not the chaining-like artificial neural networks; the temporal selectivity of activated neurons alone in response of serial order retrieval or execution is not adequate to simply account for an inter-item association mechanism forming a chain of neurons. However, although the discussed studies have shown evidence for preferential neural tuning in encoding and/or representing serial order, they have not addressed a neural mechanism accounting for parallel planning of movements as postulated by CQ.

Averbeck and colleagues (2002) were the first to provide compelling neural data supporting a parallel mechanism of neural code for serial order from planning to execution. The authors trained two monkeys in drawing different geometrical shapes. During test, they conducted multi-unit recordings from the prefrontal cortex while monkeys copied a shape on a trial-by-trial basis. A trial started with a delay period (1 or 2 s) providing no information of which shape should be drawn. After the end of the delay period, the target shape appeared on the screen and the monkey

had to copy the presented geometric by drawing a sequence of strokes. Each drawing was performed in several trials within a block until completed so that the monkey acquired prior knowledge during the delay period of which shape would have to draw. This allowed the monkey to prepare the target shape before starting the movement. The authors performed a classification analysis by training the classifier in neural patterns of each event across a drawing production (segment 1, segment 2, and so on) and tested in neural patterns across a trial (delay, Go, segment 1, segment 2, and so on) to calculate the probability of each pattern belonging to each event, i.e., movement segment. They found distinct neural patterns per movement segment which were activated in parallel for the whole delay period (Figure 2; Averbeck et al., 2002). These preserved a rank order of representation probability depending on their serial order of performance, especially toward the end of the delay period. Namely, the first movement segment had the strongest pattern probability, the second less strong etc., yet they were simultaneously activated. After the 'go' signal the segment trajectory profiles changed in that the segments' representation strengths peaked serially during execution following the produced serial order of movements. Strikingly, the distinct neural pattern of each segment in the preparatory activity could predict their correct serial order during execution. In addition, once a segment was executed as manifested by reaching its highest strength representation during execution, its representation attenuated to zero indicating deletion from the neuronal planning map, as predicted by the CQ account. These data are also consistent with a partial normalization function of neural activation such that activation across the planned movement segments was reduced as a function of their number. The latter finding is in line with other non-human primate studies using delayed response tasks where total parallel neural population activity of plans in the monkey superior colliculus (Basso & Wurtz, 1998) and the PMd (Cisek & Kalaska, 2002) is reduced as the number of possible upcoming targets is increased. Finally, further analysis of the serial order error performance during drawing execution in the Averbeck et al.'s (2002) study replicated a percent correct U-shaped serial position curve as per the simulations of CQ class models (Figure 3; Averbeck et al., 2002). In these short sequences (3-5 segments/elements), middle segments were more prone to errors than earlier or later segments. These serial position curves correlated with the strengths of neural representations such that representation strengths of the first and last positions were higher than those of the middle positions. Last, analysis of the error patterns showed that whenever a stroke segment was produced in an incorrect order it was less likely to have been classified in the correct serial position during planning (Figure 4;

Averbeck et al., 2002). These behavioral data and their neural correlates strengthen the importance of the preparatory neural activity during motor sequence planning as carrying a code for serial order and being potentially a predictor for subsequent performance at least at the level of correct serial order production.

Following a similar approach of neural pattern classification of sequential movements from planning through to execution, Kornysheva et al. (2019) recently reported neural pattern trajectories of keystrokes in humans while producing movement sequences from LTM. Here, participants were trained to produce from memory discrete five-element finger sequences of unique spatiotemporal identities: identical order but different timing structure (varied temporal inter-press intervals; IPIs), identical timing structure but different order. An abstract image at the beginning of a trial invoked a preparation period (1.8-2.2 s) and was paired with a subsequent spatiotemporal sequence identity. This allowed participants to learn which image signified which sequence and, through training, prepare the target sequence once they saw its respective image. Following sequence training, whole-brain magnetoencephalography (MEG) data were acquired during test and analyzed to determine the probability of the averaged neural pattern extracted a few milliseconds before each finger press belonging to each press position (1st to 5th). The authors found that, during the final second of planning, movement-related press positions were decoded based on their serial position of the target (planned) sequence. Similar to Averbeck et al.'s (2002) findings, after the 'go' signal the patterns were serially unfolded over time. Referring to the activation gradient of a CQ network, the preparatory neural pattern of press positions consisted of distinct pattern probabilities of different weights following a rank order which corresponded to the planned serial positions (Figure 5a; Kornysheva et al., 2019). Moreover, the CQ pattern during planning was preserved for both sequences with same finger order but different timing structure and sequences with same timing but different finger order suggesting a high-level code for ordinal position independent of effector and timing. The authors postulated that this may reflect the neural readout of overlapping representations in a temporal context layer similar to the simulations of Burgess and Hitch (1999). Interestingly, the CQ pattern correlated with subsequent sequence performance with individuals presenting a 'shrunk' CQ pattern during planning (averaged decreased distance between adjacent patterns of press positions) performing worse in terms of finger and temporal errors during sequence production. By contrast, those with a well-separated CQ signal characterized by larger distances between neural patterns, were predicted to be more accurate during production. This suggests that

a well- or poorly-planned sequence due to strong or weak connections, respectively, between a moving timing signal and position formed during learning might have caused this modulation of the CQ signal. However, a separate role from position of how planned sequence timing may have affected the distance of CQ patterns was not addressed in this study. Finally, source reconstruction revealed that the preparatory CQ signal and the press decoding patterns during production were identified in the right parahippocampal gyrus (PhG) and the ipsilateral posterior cerebellum. The contralateral sensorimotor regions were involved only in the production period.

The above studies are considered benchmarks for identifying a potential neural code for serial order supported by parallel preactivation of upcoming movements in non-human and human primates, in line with the CQ account. Monkeys in Averbeck et al. (2002) were extensively trained in a delayed-response visuo-spatio-motor task. During test, they underwent 30 iterations of the same trial for each shape so after the first few trials they knew which shape was upcoming. This means that the monkeys most likely maintained the shape in WM across repetitions of the same trial. Being, on the other hand, trained to perform the strokes for each shape in a particular order, the animals retrieved the serial order from LTM, and during the execution period they started copying the shape. On a different paradigm, participants in Kornysheva et al. (2019) were trained for two days and were given the initial visual sequence cue (abstract image) to retrieve and prepare the respective sequence entirely from memory without any visual guidance after the 'go' signal. Similarly, then, this indicates that they accessed the episodic traces of sequence representations from LTM via the episodic buffer of the WM system (Baddeley, 2000, 2012). A commonality is that both tasks employed a sensory signal (implicit or explicit) that triggered neural activity during the delay period which included some information processing of maintaining or transferring the movement plans into WM and programming some sensorimotor transformation (Funahashi, 2015) before execution.

The detection of movement representations in the prefrontal cortex before movement execution found by Averbeck et al. (2002) is in line with data signifying the role of this area in several functions. Specifically, neurons in the DLPFC present tonic sustained activity (persistent spiking rate; Fuster & Alexander, 1971; Kubota & Niki, 1971) in the delay period during processes of WM (Funahashi et al., 1989; Fuster & Alexander, 1971), reward anticipation (Leon & Shadlen, 1999; Shuler & Bear, 2006; Watanabe, 1996), rule encoding (Wallis et al., 2001), and tuning of goal-directed behavior (Kim & Shadlen, 1999; Schall & Hanes, 1993). This is possibly attributable to

an attempt of the central nervous system to handle delays between stimuli or integrate useful information (Kim et al., 2021). Critically, it has been suggested that the DLPFC acts as a mediator for maintaining representations of motor plans stored in more posterior cortical areas (Curtis & D'Esposito, 2003; Lara & Wallis, 2015). In addition, the orderly organization of movement representations in this region during planning (Averbeck et al., 2002) may well reflect differentiated prefrontal single cell activity specific for processing the temporal order of co-activated planned movements depending on their position during the delay period (Funahashi et al., 1997; Naya et al., 2017). Such distinct neuronal activity patterns may be supported by inhibitory interactions between pairs of co-activated prefrontal neurons whose firing peaks at different timing (Constantinidis et al., 2002).

The cerebellum plays a complex functional role in motor planning (Casartelli et al., 2017; Gao et al., 2018), cognitive monitoring and execution (Cui et al., 2000; Leiner, 2010; Manto et al., 2012), and the control of timing (D'Angelo & De Zeeuw, 2009; De Zeeuw et al., 2011; Doya, 2000; R. B. Ivry & Keele, 1989; Richard B. Ivry et al., 2002; Knolle et al., 2013; Teki et al., 2011). It has also been proposed that in early stages of motor sequence learning the cerebellum is a significant moderator in the cerebello-thalamo-cortical loop for optimizing sequence execution (Caligiore et al., 2019). It does so by selecting fine-grained neuronal patterns which are key for recalling constituent movement elements and communicates with the BG (Bostan et al., 2010) which, through the cortico-striatal-thalamo-cortical loops, integrate the individual motor plans into a sequence. From all cerebellar regions, preparatory activity before movement onset has been found to be dependent on the cerebellar nuclei (Chabrol et al., 2019; Gao et al., 2018), while the ipsilateral anterior lobe and posterior volume, lobule VIII, represent sensorimotor information (Stoodley & Schmahmann, 2010, 2018). Specifically, the latter regions have been shown to be functionally connected to the sensorimotor cortices (Bernard et al., 2012; Habas, 2021; Krienen & Buckner, 2009; O'Reilly et al., 2010; Xue et al., 2021) with mapping neuroimaging (Bushara et al., 2001; Debas et al., 2010; Grodd et al., 2001, 2005; Guell et al., 2018; Guell & Schmahmann, 2020; Orban et al., 2010; Rijntjes et al., 1999; Van der Zwaag et al., 2013; Wiestler et al., 2011) and stimulation (Mottolese et al., 2013) studies agreeing that these encode finger representations supported by cerebello-cortical loops (R. M. Kelly & Strick, 2003). Thus, the cerebellar origins of the CQ signal during sequence preparation found in Kornysheva et al. (2019) indicate cerebellar contribution already before movement onset to the control of effector-related sequence production.

On the other hand, the hippocampus and surrounding parahippocampal structures participate in procedural memory processing which mediates early motor skill acquisition and the learning and consolidation of sequential information through connections with the prefrontal cortex and the striatum (Albouy et al., 2013). The implication of the PhG in the formulation of the preparatory CQ signal (Kornysheva et al., 2019) rather points to the contribution of this structure in first-order (as opposed to the prefrontal cortex) encoding and retrieval of concatenated events in a temporal order, as shown in decision-making sequence execution (Shahnazian et al., 2021) or episodic memory tasks involving sequence rehearsal in human (Ekstrom et al., 2011; Lehn et al., 2009; Lieberman et al., 2017) and non-human primates (Naya et al., 2017). This resonates with a proposed framework positing that the hippocampal system is a higher-level controller in a hierarchy of brain areas participating in sequence representation: It acts as a 'general-purpose sequence generator' that links together events, successively experienced in time, without encoding detailed information about space and time (Buzsáki & Tingley, 2018; Friston & Buzsáki, 2016).

A few other studies have addressed the parallel representation in the context of CQ processing of sequential movements. Behmer and colleagues (2018) reported online excitation of produced movements, namely *during* sequencing in a copying-typing task, providing indications of parallel preactivation of all movements. The authors recorded motor evoked potentials (MEP) triggered by transcranial magnetic stimulation pulse (contralateral motor cortex) while participants used the right index finger assigned to different serial positions in five-element sequences of words or random non-words. MEPs, elicited at the onset of the press, showed decreased activation as a function of 2nd to 5th positions, reflecting cortico-spinal excitability related to the currently produced response. This indicates that movements were activated in parallel though at different levels. Of note, it is possible that this study captured the output state of each movement associated with each sequence position reflecting the competitive cue of elements determined by their excitation level once selected and while executed. This is in accord with behavioral findings based on a similar task showing that RTs of probed sequence positions during typing increase with position number (Behmer & Crump, 2017). It is unlikely that MEPs readout reflected serial inhibition, as, according to the CQ prediction, an action is self-suppressed only after it is executed. That said, the predicted serial inhibition would be anticipated to be independent from serial position with all position-related MEPs being invariant. A design based on a paired-pulse transcranial magnetic stimulation protocol (Kujirai et al., 1993) would be useful for acquiring such a measure probing

the GABAergic inhibitory dynamics associated with each press position. In addition, to directly investigate parallel preactivation, such a protocol would give insights into the preparatory state of each movement (Bestmann & Duque, 2016). As several studies report, MEP amplitude increases about 100 ms before effector-related muscle activity (e.g., Chen et al., 1998; Leocani et al., 2000), the excitatory movement state-changes would be expected to mirror the activation gradient, i.e., the differentiated co-activation of all forthcoming movements depending on their position.

At the cortical level, lateralized readiness potentials (LRPs; see Schurger et al., 2021) acquired with electroencephalography (EEG), were shown to linearly increase with keystroke number (Pinet et al., 2019). Specifically, in preparation of unimanual keystrokes, ~200 ms prior to movement onset, a two-element sequence exhibited a twice as high amplitude than a single keystroke. With no additional data available from longer sequences, we should be cautious in inferring a clear sequence length effect on LRP which would putatively reflect graded preactivation of forthcoming movements. In the same experiment, a bimanual two-element sequence elicited bilateral LRPs of same amplitude. Indeed, this slow negative potential, originates in the M1 contralateral to the performing limb (Lüder Deecke et al., 1969) and is associated with motor programming and execution (Shibasaki & Hallett, 2006). Therefore, the above LRP findings are in support of the idea that the brain prepares multiple intended movements in parallel in accord with the motor programming hypothesis and the CQ account, with a tendency for a rank order representation of unimanual sequences even at the very final stage of a delay period before motor engagement. Additional research on the LRPs as an index of late-stage motor preparation has highlighted the possibility of a limited scope of planning multiple upcoming movements at later positions in lengthy word sequences (Scaltritti et al., 2018). In a copying-typing serial task, the related LRPs were found to be invariant when a late position (6th or 7th) was probed using the alternate hand as opposed to LRPs probing early positions (2nd or 3rd). If, however, the planned sequence elements are competitively cued, it is highly likely that not only are they processed in parallel, but movements associated with later positions are significantly inhibited in the competitive choice layer by the strongest candidate action to the extent that response-related motor cortical activity is not captured by LRPs.

It is indeed an interesting observation that a CQ parallel processing has been shown to be traceable across different species, brain areas, and modalities. Bhutani et al. (2013) directly inves-

tigated the role of BG in the conversion of concurrently pre-planned saccades into a correct sequence during execution. By applying deep brain stimulation in bilateral subthalamic nuclei of patients with Parkinson's disease and, conversely, silencing the caudate nucleus in monkeys, while performing a double-step saccade task, the authors revealed that disinhibition of these BG neurons compromises the execution of saccades in the correct order. Previous behavioral work of the same group demonstrated that competing saccades are mutually inhibited so that the one associated with the first target is completed first (Ray et al., 2012), while the upcoming saccades are still activated in parallel as the sequence unfolds (Bhutani et al., 2017). The above data (Bhutani et al., 2013) suggest that the substrate of this competitive inhibition lies in the BG inhibitory neurons. In a CQ network, they appear to contribute to the cueing of movement plans in the competitive choice layer ensuring that the most active plan manages to inhibit the others in order to be selected for execution. In addition, the frontal eye field area is implicated in the preservation of the partially activated representation plans. These prefrontal neurons have been shown to be concurrently responsive to two planned saccades by differentially encoding an upcoming plan while the first is being executed (Basu & Murthy, 2020; Jia et al., 2021), providing neurophysiological support of the Bhutani et al. (2017) behavioral data.

1.2.2 Mechanisms of motor timing

Time-based CQ models (e.g., see Burgess & Hitch, 1999) posit that control of order, in the form of ordinal position, depends on a timing signal that moves over time regulating the position a sequence element associates with and thus ensuring a correct serial order output. This implies that during sequence encoding (e.g., learning or sequence presentation in ISR conditions), the temporal structure of a sequence is mapped on a temporal context controller of the network so that the inter-item timing interval variations would guide the timing (i.e., rhythm) of the serially output sequential elements. Such a CQ architecture in which timing is integrated by interacting with position, suggests that order and timing are interwoven core features of sequence learning and control reflecting inseparable processes. However, diverse empirical data – from behavioral to neuroimaging – suggest that sequence order and timing are likely to be represented independently.

The possibility that spatiotemporal information may be integrated during sequence learning has been investigated by Shin and Ivry (2002). In a serial reaction time task, participants produced

temporal sequences, defined by response-stimulus intervals, and ordinal sequences of visual stimuli. The two features were considered as learnt concurrently because incidental temporal learning occurred only when a temporal sequence also included spatial information. However, to measure the level of learning, the authors used the response-stimulus intervals which are heavily embedded to the participants' RTs and not the inter-stimulus intervals (Ullén & Bengtsson, 2003). In addition, these experiments used incidental temporal structures, with the authors noting that an independent temporal representation is possible once a clearcut temporal pattern is learnt. Ullén and Bengtsson (2003) addressed the modular profile of spatiotemporal representations in well-learnt single-finger key sequences. Different sequence conditions were learnt and later produced from memory by independent groups of participants in different orders. One group first learnt a combined sequence consisting of multiple key presses and certain temporal intervals, then a temporal sequence made of the timing structure of the combined sequence but involving one key only and last an ordinal sequence with the ordinal structure of the combined sequence but isochronous timing. The other group learnt the same sequences but ordered as temporal, ordinal, and last combined. This manipulation revealed that learning a combined sequence first acted as an overarching base for benefiting the learning of the temporal and ordinal sequences. Importantly, participants not having benefitted by this facilitation (second group) performed better in the combined sequence, suggesting that they had developed independent representations of order and timing that was transferred to the combined sequence. In a second experiment, it was shown that an ordinal structure with random timing can be learnt independently of a certain temporal structure and random order.

Readiness potentials from EEG data add more support to an account for independent processing already from the preparation period of uncued sequential movements (Bortoletto et al., 2011). Here, the preparation process for a six-element sequence with a demanding (non-isochronous) temporal structure but simple ordering started earlier relative to sequence initiation than for an equal-length sequence consisting of a complex order but isochronous timing. At the behavioral level, RT research has shown that when the ordinal structure is known in advance but not the temporal structure, RTs are faster compared to prior knowledge of the temporal structure but not the ordinal one, with the effect being more pronounced in sequences with increased temporal complexity (Maslovat et al., 2018). This dissociation suggests that prior to movement onset the preparatory process supporting sequence timing might be more demanding than that supporting sequence ordering. That order and timing are independent was corroborated by further behavioral

findings demonstrating that temporal transfer evolves in new ordinal sequences only after the latter becomes familiar (Kornysheva et al., 2013). Neuroimaging data confirm that this independent representation is supported by different brain areas. Bengtsson et al. (2004) found that control of temporal order is related with increases in blood oxygenation level-dependent (BOLD) response in the pre-SMA, the precentral sulcus, the temporal lobes, and the contralateral inferior frontal gyrus. On the other hand, ordinal structure processing elicited fronto-parietal and cerebellar activations, as well as increases in the BG. A more thorough investigation of temporal and ordinal encoding *vs* an integrated encoding was conducted in a fMRI study using muti-voxel pattern analysis (MVPA) (Kornysheva & Diedrichsen, 2014). This method allowed for identifying differentiated neuronal activity associated with certain sequence conditions, during the production of well-learnt sequences from memory. MVPA revealed that the only region that accounted for integrated encoding of ordinal and temporal structure was the contralateral M1. The premotor (PM) cortex and parietal cortex showed differentiated encoding of independent representations, with the PMd carrying information about the ordinal structure and the ventral PM encoding the temporal structure. This finding is consistent with data showing that M1 is associated with a higher-order processing of sequence representation: As soon as M1 receives input from the premotor cortex, it combines the constituent sequence information and then tunes to the demands for movement execution (Yokoi et al., 2018).

The above empirical findings indicate that the sensorimotor system relies on a timing mechanism that allows for a flexible control of movements over time ensuring well-timed initiation and correct temporal production (Remington, Egger, et al., 2018), without being hardcoded with the order of movements. Several studies over the recent years have provided insights into the neural computations underlying such a flexible control (García-Garibay et al., 2016; Jazayeri & Shadlen, 2015; Merchant et al., 2011; Ohmae et al., 2013; Remington, Narain, et al., 2018; Takeya et al., 2017; Wang et al., 2018), by mostly studying cortical ramping activity. Ramping (or climbing) activity is a type of neuronal activity characterized by reliable firing rate dynamics as a function of time (Merchant, Harrington, et al., 2013; Narayanan, 2016). Ramping is said to capture temporal information and is commonly found in timing tasks (Narayanan & Laubach, 2009; Parker et al., 2014) as its ramping profile matches the time boundaries of an interval (i.e., activity either increases or decreases in a consistent manner from the beginning till the end of the interval).

Climbing cell dynamics have been reported to be part of circuits involving cortical and subcortical regions that support a central timing mechanism which paces interval timing of motor responses (see Merchant, Harrington, et al., 2013). Non-human primate studies outline the profile of this type of spiking activity in the medial PM cortex using the synchronization-continuation tapping task (Zarco et al., 2009). Different populations interact during timed behavior, yet preferentially spike in alignment with motor responses (Perez et al., 2013), before motor response onset, relative to next motor response, and relative to previous one (Merchant et al., 2011). Additionally, Jazayeri and colleagues have reported ramping dynamics in the non-human primate brain during temporal interval motor tasks involving either eye movements (Jazayeri & Shadlen, 2015) or both eye and hand movements (Wang et al., 2018). When monkeys underwent a stage during which they had to 'measure' a time interval, ramping activity in the lateral intraparietal cortex started over once they progressed to the next stage where they had to reproduce the previously perceived time interval. The reproduction-related ramping activity increased to a degree that it correlated with the measurement-related ramping activity (Jazayeri & Shadlen, 2015). Importantly, the authors found very diverse response dynamics across single neurons and populations in the medial frontal cortex, albeit conforming to a common temporal behavior, that of scaling (Wang et al., 2018). Temporal scaling was evident on a trial-by-trial basis where activity became slower or faster depending on whether the animal was producing a long or short interval, respectively. These findings suggest that response dynamics supported by ramping activity in timing tasks can predict previous or forthcoming events over time (Cadena-Valencia et al., 2018; Kaufman et al., 2016; Tiganj et al., 2018).

Further, recent data by de Lafuente et al. (2022) demonstrate that a possible mechanism underlying temporal scaling capacity may be an internalized metronome which controls and flexibly adjusts the tempo to the temporal demands of the task. Here, monkeys underwent entrainment periods with a presentation of a visual stimulus (metronome) shifting from left to right at three different tempos. Immediately after, maintenance of these tempos was required in a period ranging from one to six intervals, where the visual metronome was no longer present, and no movement was performed. At the end of the trial, the animals had to indicate the estimated location of the visual metronome on the screen. Spiking activity from six brain areas (SMA, prefrontal cortex, lateral and medial parietal lobe, visual cortex, and the hippocampus), revealed that not only were

oscillations present during the entrainment period but also during maintenance. Critically, oscillatory activity was scaled (compressed or stretched out) to match the target tempo as initially instructed by the metronome and could predict behavior. The authors found that although this mechanism was distributed across the recorded areas, there was a hierarchical differentiation in how these represented the putative internal metronome. The visual and lateral parietal areas could encode more the spatial (location) but not the temporal aspect (tempo/speed) of the metronome, whilst SMA showed the exactly opposite pattern, followed by the prefrontal and the medial parietal areas. The hippocampus was sensitive to following the alternation of the metronome (from left to right and so on), producing different trajectories. As noted by the authors, the latter finding supports the argument that the hippocampal system is a high-level sequence controller not encoding task-specific information about the what (spatial) and when (temporal) of a sequence of events (Buzsáki & Tingley, 2018).

At the behavioral level, Hardy et al. (2018) extensively trained human subjects in a tapping task to repeatedly produce a single word at three different speeds, normal speed, twice as fast, and twice as slow. During test, reproduction of the learnt word was required without any cues (i.e., no visual or auditory targets were present). It was found that participants were able to speed up or down the acquired temporal pattern as shown by a scaling index measuring the degree of correlation between the normal and scaled (slow and fast) tempos. Another behavioral experiment showed that training can improve temporal precision depending on different speeds and, ultimately, scaling (Slayton et al., 2020). Specifically, using a similar task as in Hardy et al. (2018) for studying the temporal performance of musicians *vs* non-expert musicians, Slayton and colleagues found significant temporal scaling effects in the former group from the beginning of training. While non-experts struggled at early stages of training, they improved their temporal scaling capacity over the course of training, in line with prior behavioral findings of a training effect on temporal scaling improvement (Keele & Summers, 1976; Summers, 1975). Both experiments found a Weber-speed effect, i.e., more temporal precision (smaller variability) when producing a motor sequence at a faster than a slower tempo.

A few researchers have attempted to explain temporal scaling data, discussed above, by using RRN models. For example, Wang et al. (2018) successfully simulated the findings of temporally scaled ramping activity by manipulating an external input that triggered[3] the individual neurons and controlled the following recurrent dynamics within specific temporal boundaries. Specifically, temporal scaling in this ramping RNN model was achieved by using two fixed points at the time of initialization, defining the start and end of the speed. The input that governed the speed was an external cue input at different speeds which was used to train the model. This simulation outcome together with the largely variable response dynamics found in Wang et al. (2018) is at odds with a prominent class of population-clock neural network models of timing. The latter hold that timing is generated by a population clock which is made of a neuronal chain, i.e., a chain of activated neurons within a population. In a busy neuronal population with time-varying firing rates, each time point can be coded by the specific activity of individual or a group of neurons. In turn, to produce a motor response at certain timing, output neuronal activity can be trained to identify activity patterns and read time (Buonomano & Karmarkar, 2002; Buonomano & Laje, 2010; Mauk & Buonomano, 2004). A popular representative RNN model based on population-clock dynamics was trained in producing words and was able to generate spatiotemporal patterns with accurate timing (Laje & Buonomano, 2013).

Accordingly, Hardy et al. (2018) implemented a population-clock RNN model for simulating the behavioral findings of temporal scaling effects using aperiodic temporal patterns at different speeds. The authors build a network with high-dimensional activity and tackled the disadvantage of limited LTM capacity by updating the weight's values of each input at high time-resolution rate. In this way, extensive training of the model ensured the generation of stable trajectories encoding reliable temporal patterns and producing the trained patterns, returning afterwards to a rest state. One external cue input served to start each trial and a second one was the speed controller, namely a tonic speed input that modulated the temporal dynamics based on which the network was trained. As a result, the model successfully predicted both the temporal scaling and the Weber-speed effect behavioral data.

[3] Of note, in such nonlinear activation functions, output from this activation moves to the next hidden layer and the final output is determined by the forward (outputting values from one hidden layer to the next) and back-propagation (correcting the final output values based on the forward propagation output and repeating the process) processes.

The contrast between the ramping RNN (Wang et al., 2018) and the discussed population-clock RNNs regards that these are different timing models, the dedicated and intrinsic models, respectively. These centre around the debate on whether timing relies on dedicated mechanisms of the brain or on intrinsic computations that allow timing to emerge from any neuron (see Paton & Buonomano, 2018), for which a full review is beyond the scope of this work. In the simulations by the Buonomano group (e.g., Goudar & Buonomano, 2018; Hardy et al., 2018; Laje et al., 2011; Laje & Buonomano, 2013), timing emerges solely from the active state of the network, whereas Wang et al.'s (2018) simulations of ramping activity rather suggest a common mechanism (e.g., de Lafuente et al., 2022) since populations were very variable but merged to produce temporal scaling without the need of gated trajectories.

The above empirical data suggest that order and timing are most likely independent, not interacting, processes with timing being controlled by a dedicated mechanism common across neuronal populations or intrinsically. Consistent with a modular CQ architecture (Zeid & Bullock, 2019), a CQ representation of serial order could reconcile with a dedicated mechanism which would adjust the tempos of parallel plan representations after the plans in the network's parallel planning layer have been tuned to positions during learning via a positional context layer (Houghton et al., 2022).

1.2.3 What can we learn from planning period dynamics and how?

Motor planning is a pre-movement state that encompasses a number of processes necessary for optimizing the intended forthcoming movement in order to interact effectively with the environment (Rosenbaum et al., 2004). These processes can be implicit or explicit learning parameters (*cf.* ordinal and timing parameters of the intended movements, discussed above), memory (Sheahan et al 2016), action selection (Cisek, 2007; Gallivan et al., 2015, 2016), multisensory integration (Sober & Sabes, 2003, 2005) and decision-making (Wolpert & Landy, 2012) processes. An overwhelmingly increasing amount of data from different measures, modalities and methods has been giving insights into the functional and mechanistic role of motor planning in relation to subsequent execution.

1.2.3.1 The current debate: Reaction time as a marker of motor preparation

The above definition makes planning a broad term for describing such a wide range of processes that may be concurrent to strictly movement-related ones. It has been argued that motor planning *per se*, i.e., preparatory processes that are solely movement-related, should be considered as devoid of any higher-order functions (Haith & Bestmann, 2018; Wong et al., 2015). The latter processes are proposed to participate in an initial high-level stage for achieving movement generation by identifying and establishing a motor goal to guide the desired movement outcome. According to this view, this entire composite process constituting the 'what' pathway, is time-consuming and thus may be responsible for variations in RTs before engaging in movement initiation. Subsequently, once a motor goal has been defined, the motor system starts to plan the specifications of the movement (kinematics, action selection, control of motor commands) necessary to achieve the motor goal through a 'how' pathway. According to the authors, it is that low-level pathway which defines motor planning and accounts for very little preparation time. The above framework led to the hypothesis that motor planning is instantaneous, undergoing a continuous update based on the ongoing formed motor goals, action selection or direction, and evaluation of the benefit (Wong et al., 2015). Part of this thesis has been based on challenging RT as a measure of representing better or more complete movement preparation.

The prominent view on the functional role of RTs is that it reflects the time needed to compute the appropriate parameters for delivering an optimal response. Traditional studies of motor programming have shown that preparation of more demanding movements was associated with increased RTs (Henry & Rogers, 1960; Sternberg et al., 1978). Rarely this behavioral readout is studied independent from a preceding delay or preparation time. Effects of in advance (i.e., preparation) time on response time have shown RT decreases with longer preparation periods (Dahan et al., 2019; Riehle & Requin, 1989; Rosenbaum, 1980). Additionally, knowing in advance before the 'go' signal what movement to make, reduces the RT to movement initiation (Rosenbaum, 1980).

Haith et al. (2016) investigated the time required to prepare a movement in an attempt to provide a mechanistic understanding of when a movement is ready to be generated by dissociating it from the latency to initiate the movement. The authors showed that movement preparation could occur earlier than movement initiation; participants accurately made faster reach movements in a forced RT condition about 80 ms earlier than their baseline RT. This means that participants made

use of less preparation time for producing just as accurate movements. Longer baseline RTs were not necessary as did not contribute to actual movement preparation. Instead, as commended by the authors, this extra RT time might have served for avoiding potential imprecise movements. In keeping with these observations, Wong et al. (2016) found that planning a movement trajectory came with an RT cost compared to a cued trajectory in which a plan was not necessary. This RT difference was interpreted as reflecting the representation of the planned movement. The first study advocates that only a small percent (~15 %) of the interval from a trigger to the response accounts for some aspect of, what the authors would call, the 'what' specification of the planned movement. This then contradicts the claim that movement preparation itself is not as time-consuming as we previously thought (Haith & Bestmann, 2018; Wong et al., 2015). In addition, in volitional control of movement initiation, as opposed to forced conditions, an RT cost seems to qualify as a necessary computation time which can reach a minimum with longer preparation times (Dahan et al., 2019). The second study, on the other hand, does not provide a clear 'what - how' dissociation, as even with a small (22 %) cost in the case where an additional planning process is imposed, we cannot preclude that in both experimental conditions additional 'what' processes could have taken place during planning.

Making sense of the processes participating in a planning period is necessary for the advancement of the field as this would facilitate data interpretation and make inferences more accurate. However, more data are warranted for fully understanding the composite nature of motor planning and its imprint on RT.

1.2.3.2 Prediction of upcoming actions and performance level from planning dynamics

A plethora of evidence supports that motor planning encodes valuable information for predicting upcoming movements and quality of performance. Utilization of motor programs during planning benefits skilled motor learning (O'Shea & Shenoy, 2016) and sequence performance (Keele, 1968; Rosenbaum, 1985, 2010), affecting movement time, speed, and accuracy (Al Borno et al., 2020; Haith et al., 2016; Klapp, 1976, 1995, 2003; Klapp & Erwin, 1976; Riehle & Requin, 1989). As discussed previously, multiple motor plan representations of different weights have been found to be activated in parallel during planning predicting forthcoming movements and sequence performance after movement onset (Averbeck et al., 2002; Kornysheva et al., 2019), in accord with the CQ account. In both studies, the parallel movement-related neural patterns predicted both

the serial production of planned movements and the level of performance in terms of accuracy. Accordingly, motor sequence learning and performance has been shown to benefit from optimized planning of multiple sequential movements (Ariani & Diedrichsen, 2019). Specifically, participants were trained in a discrete production task to produce visually cued five-finger sequences as fast as possible. Preparation duration was manipulated by indicating the 'go' signal for sequence initiation at different time points within the preparation period. It was found that longer preparation durations resulted in faster sequence execution for well-learnt sequences. At the same time, preparation time was reduced indicating that participants were gradually able to plan these sequences both faster and more accurately. This faster preparation encompassed the planning of the first three to four movement elements, planning the rest 'online', during execution. This was found regardless of training level and possibly indicates a ceiling effect in how many elements can be planned before initiation, especially since longer preparation times did not improve this capacity (i.e., planning the entire sequence). This finding was corroborated when advance knowledge of a certain number of elements of upcoming long sequences was given (Ariani et al., 2021). This revealed that knowing on average up to three movements ahead positively affected subsequent performance. Further, an fMRI investigation has shown that preparatory sequence finger-specific activity originates in contralateral primary somatosensory cortex (S1), similar to M1, and could predict the planned upcoming action (Ariani et al., 2022). Similarly, Gale et al. (2021) found changes in the neural states of M1 and S1 with both areas encoding effector-specific information during motor planning. These findings suggest that S1 prepares the system for processing the sensory information that comes with the intended action.

1.2.3.3 Neural oscillations show differentiated activity during planning *vs* execution

Neural activity during motor planning at the time-frequency domain encodes task-invoked information. Specifically, pre-movement oscillatory dynamics show distinct patterns of activation relative to peri-movement[4] activity. Gamma oscillations originate from local field potentials which rhythmically fluctuate at high frequencies (> 30 Hz, but typically > 60 Hz) (Buzśaki & Wang, 2012; Fries et al., 2007; Kropotov, 2016a). They have been reported in the hippocampus (Colgin & Moser, 2010) and the human motor cortex (Cheyne et al., 2008; Crone et al., 1998; K. J. Miller et al., 2007; Muthukumaraswamy, 2010; Pfurtscheller et al., 2003; Szurhaj et al., 2005). Increases

[4] Activity just before movement onset, during movement, and immediately after movement is completed.

in hippocampal and prefrontal gamma activity reflect the increased load of recalled events retained in WM during delay periods in neurosurgical patients (Howard et al., 2003; Van Vugt et al., 2010) and healthy participants (Roux et al., 2012). On the other hand, the movement-related gamma synchronization (MRGS), starting ~ 0.05 s before up until ~ 0.1 s after movement onset, is typically localized in the contralateral precentral gyrus (M1) (Cheyne et al., 2008; Gaetz et al., 2010, 2011; Muthukumaraswamy, 2010) and the SMA (Wilson et al., 2010). The MRGS is thought to be the oscillatory marker of movement execution, given its focal localization and its temporally transient bursts. Essential work on the functional profile of the gamma rhythm involved the investigation of various types of movements (slow movements, repetitive or ballistic abductions, and static contractions under different conditions) (Muthukumaraswamy, 2010). These experiments revealed that each individual movement elicited MRGS at its onset and this activity was not preserved through the end of the movement, suggesting that MRGS signifies motor onset response.

Another prevalent rhythm of the motor circuitry is the beta rhythm (14–30 Hz) which is important for motor planning (Heinrichs-Graham & Wilson, 2016; Little et al., 2019; Park et al., 2013; E. Rhodes et al., 2018; Sanes & Donoghue, 1993; Turella et al., 2016; Tzagarakis et al., 2010, 2015) and execution (Bizovičar et al., 2014; Tatti et al., 2020), and the temporal control of rhythmic movements (Merchant & Bartolo, 2018).

Motor cortical beta activity, together with the motor-related μ-alpha range (mu rhythm; 8–13 Hz; Gaustaut, 1952), presents with short attenuation of oscillations, termed event-related desynchronization (ERD). Compared to mu decreases, beta-ERD shows the strongest responses during sensorimotor processing and movement preparation and execution and its latency depends on movement time; it is observed ~ 1 s before movement onset until ~ 0.5 s after the end of movement where it resynchronizes (event-related synchronization; ERS; also termed the post-movement beta rebound) (Pfurtscheller & Aranibar, 1977; Pfurtscheller & Lopes Da Silva, 1999), suggesting possibly a clearing-out of the motor plan to prevent ongoing sensorimotor processing (Hervault et al., 2021). These 8-30 Hz ERD/ERS dynamics are considered correlates of cortical excitation/inhibition, respectively, modulating changes in corticospinal excitability (Bergmann et al., 2019; Hussain et al., 2019; Thies et al., 2018). Both mu- and beta-ERD show lateralization in contralateral precentral gyrus during preparation, especially in mu-ERD, and become bilateral closer to movement onset (Chatrian et al., 1959; Dujardin et al., 1993; Leocani et al., 1997; H. Li et al., 2018; Pfurtscheller & Berghold, 1989).

The functional role of beta, in particular, is not fully understood but it has been suggested to be involved in sensorimotor integration and top-down control via its intrinsic fluctuations (Barone & Rossiter, 2021; Engel & Fries, 2010). Although otherwise known as the sensorimotor rhythm, beta activity is widespread implicating other areas apart from the precentral gyri, such as the SMA (Cheyne et al., 2006; Wilson et al., 2010), parietal (Cheyne et al., 2006; Heinrichs-Graham & Wilson, 2015), premotor (Cheyne et al., 2006) and prefrontal cortices (Heinrichs-Graham & Wilson, 2015; Lundqvist et al., 2016; Wessel et al., 2013), the BG (Leventhal et al., 2012; Mirzaei et al., 2017; Stein & Bar-Gad, 2013), and the cerebellum (Wilson et al., 2010). This suggests the complex role of beta in cognitive alongside sensorimotor processing for efficient executive control and memory handling in task performance (for a review and discussion, see Schmidt et al., 2019).

1.2.3.4 A mechanistic understanding of motor planning: Outstanding questions

The Georgopoulos group (Averbeck et al., 2002) and Kornysheva and colleagues (2019) provided evidence of parallel activations of planned movements over a delay period prior to sequence execution and serial activations once the movement sequence started. Using decoding techniques, they computed the probability of each action being activated over both periods and found that the probabilities ranked in parallel over preparation and then peaked serially over execution, both based on ordinal position. This decoded movement-related activation suggests that their movement elements were prepared and executed independently. As these were over-learnt sequences, motor chunking (unification of elements in one representation) could have occurred even when a temporal structure was indirectly imposed during production via feedback (Verwey & Dronkert, 1996) as in Kornysheva et al. (2019). Do then the observed distinct activations from preparation to production refute the assumption that those movements might have been chunked (because chunking would be expected to yield a single neural pattern representation across planning and execution)? More importantly, is there a common principle under which neural preparatory activity and execution operate, regardless of the number of movements one prepares and produces or whether a sequence has been transformed to a chunk or not? Zimnik and Churchland (2021) recently attempted to address this question by investigating the role of motor cortex (M1 and PMd) in how different movement types are planned, initiated, and executed. Monkeys were trained to produced single reaches or two-element reaching sequence either in a compound manner

characterized by rapid production or in a delayed manner where the two movements were temporally much more discrete. Both were over-learnt sequences and, in the case of the compound reaches, extensive training in combination with the minimal interval between the two movements was expected to induce motor chunking (Rosenbaum et al., 1983; Sakai et al., 2003). Population activity during preparation revealed separate time courses for each movement in both sequence conditions, as during execution. In compound reaches, this was manifested by overlapping yet distinct activities: The second movement started to prepare when the first was still being executed. In addition, single reach activity in preparation was very similar to the activity related to the first reach in the sequence conditions. These findings show that the motor system uses a flexible way to produce movements of different types using separate representations which do not merge in M1 as a chunk.

Another important question in the field of motor neuroscience has been that of what property of the preparatory activity in motor cortex defines when the system is ready to execute the response and how neurons in the same area can drive both preparatory and movement-related activity (Remington, Egger, et al., 2018; Wong et al., 2015). The account that preparatory activity is held at a corticospinal subthreshold level (Duque & Ivry, 2009), i.e. suppressed, has long been considered unlikely since animal neurophysiological data have shown no indication of inhibitory activity in those areas (Churchland et al., 2010; Kaufman et al., 2010, 2013). Instead, it has been suggested that preparatory activity is being kept constant within a *null* (sub)space of a bigger high-dimensional firing rate space representing a population of neurons, whereas movement activity becomes multi-dimensional driving the muscular system to execute the movement (Kaufman et al., 2013). Further, the same group identified a potential mechanism that accounts for neuronal populations in PMd. This area was found to hold preparatory activity output to a null space attenuating their upstream communication with M1, thus preventing activity to extend to other dimensions so to produce movement (Kaufman et al., 2014). In this framework, motor planning could be supported by preparatory activity, at an output-null state, which may choose the optimal point in the high-dimensional space based on the motor plans of the intended action. Overall, these data demonstrate that preparatory and movement activities are distinct while later work confirmed that this distinction is also supported by separate computations (Elsayed et al., 2016). Such a mechanism can explain why preparatory activity can co-exist with execution-related activity and predict

certain parameters of forthcoming movements or sequences of movements (Remington, Egger, et al., 2018).

1.3 Summary and Problem Statement

The period before we execute a sequence of movement encodes important information about its spatiotemporal features - order and timing. Specifically, sequence planning is essential for organizing movements in the correct order over specific time constraints. Neural network studies and empirical evidence provide a framework which supports that sequential elements are planned in parallel and competitively queued depending on their initial serial order. Certain CQ models suggest a central role of timing regulating serial order in the same system, despite several evidence advocating for a dissociative control. At the same time, the delay period to prepare a sequence has been linked with more accurate sequence performance. However, no studies to date have examined at the behavioral level whether a graded activation of parallel planned movements is accessible and whether it is modulated by sequence timing or preparation time. In addition, although significant steps have been made in understanding motor timing, the mechanisms of speed modulation and its relation to serial order during motor sequence planning in the human brain are yet unknown. Specifically, what the field yet lacks is a systematic investigation at the neural level of a potential integration of order and time in a common CQ preparatory mechanism or instead a dissociation which would imply a modular control of spatiotemporal motor sequences.

1.4 The Present Thesis

1.4.1 Aims and objectives

This research aimed to address one broad question emerging from reviewing the literature: What are the behavioral and neural markers of a planning mechanism which would explain how order and timing of movements are represented before sequence execution? This central question is broken down into the following aims:

The first strand of this research set out to a) identify a behavioral readout of graded availability of planned movements, following the CQ framework, and b) investigate whether this CQ preparatory gradient is modulated by the temporal structure of the planned sequence or the length of preparation time. The second strand aimed to further a) establish at the neural level, using non-invasive EEG, a CQ parallel graded activation of planned movements belonging to sequences of different speeds and b) determine either a dissociation of ordinal position from timing or an integration of those features during sequence planning.

To that end, a series of four experiments was conducted employing a within-subjects design. The first three experiments were built to address the first strand of research whilst the fourth experiment was created to cover the questions of the second strand of research. In all experiments, a novel 'delayed-production' paradigm was utilized which was created to model movement availability during planning of well-learnt keypress sequences. During sequence training, the paradigm employs the principles of the delayed movement (Cisek & Kalaska, 2002, 2005) and the discrete sequence production tasks (Verwey, 1999) to establish learning of the target spatiotemporal sequences. Its core feature is the learnt association of a unique abstract visual stimulus with a unique target sequence. During test, the corresponding abstract visual stimulus enables the retrieval and preparation of the cued movement sequence during a delay period, and its production from memory following a *Go* signal (Kornysheva et al., 2019). Through probe trials, the paradigm probes the preparatory state of constituent movement elements of the cued sequence or that of a prepared or an unprepared single movement, by means of RTs and error rates. In this motor task, across experiments, the right hand was used as the effector model performing four-element keypress finger sequences used to model discrete sequential movements.

This thesis presents and discusses only the results from data acquired from the test sessions as these were designed for addressing the research questions outlined above. Below is an overview of the scope and objectives of each experiment.

Experiment 1 – This experiment measured the behavioral availability of probed movements based on their ordinal position during the preparation of two isochronous sequences of different finger order but same – slow – timing. The key manipulation here was the varying delay time between the abstract visual stimulus and the *Go* signal. This delay constituted the preparation period. This experiment tested the hypothesis that the preparatory gradient of movement availability by ordinal position expands with longer preparation time reflecting a more accurate sequence plan.

Experiment 2 – This experiment focused on varying the sequence timing by using three sequences of identical finger order but different timing: slow, fast, and irregular. The critical manipulation of sequence timing served to test the alternative hypothesis that timing affects the preparatory gradient depending on ordinal position: The gradient would accordingly be shortened or enlarged between positions as per the temporal intervals of the planned sequence.

Experiment 3 – Same as *experiment 2*, adding the measurement of the behavioral availability of a control movement: a single press delivered by an effector not belonging to any of the target sequences. This experiment tested the additional hypothesis that such a movement may be part of the preparatory gradient but is much less available than the sequential movements.

Preparation time was not manipulated in *experiments 2* and *3*. Across *experiments 1-3*, an overarching hypothesis was tested that a more pronounced preparatory gradient would be associated with better quality of sequence performance.

Experiment 4 – Following up *experiments 2* and *3*, this experiment similarly measured the behavioral availability of probed sequential movements, focusing on sequences with the same finger order but different speeds: slow and fast. A control movement of an unrelated effector was also investigated under different conditions. Further, concurrent scalp EEG and electromyography (EMG) - as a control measure - recordings were collected on a separate session during the planning and production from memory of the sequences and a single movement (unrelated effector). Following the CQ predictions, a machine learning technique was used for decoding the EEG signal over sequence planning and execution to investigate the hypothesis of parallel graded preactivations of planned movements before execution and their potential modulation by sequence speed. Scalp EEG is a non-invasive technology for recording electrical brain activity (Berger, 1929) and is sensitive to capturing the summed activity of postsynaptic potentials generated from cortical pyramidal cells (Buzsáki et al., 2012; Nunez & Srinivasan, 2009; Erik St. Louis et al., 2016). In particular, extracting cortical EEG patterns for the aim of classifying certain task conditions using machine learning techniques for neural decoding equivalent to MVPA applied in fMRI, has been gaining ground over the last years (Carlson et al., 2019). Time-resolved EEG decoding has been applied for studying various aspects of cognitive function (J. J. Foster et al., 2015; Samaha et al., 2016) and motor control (Kikumoto & Mayr, 2018; T. Li et al., 2018; Paek et al., 2014; Tayeb et al., 2019; Yang et al., 2015; Yoshimura et al., 2017), as well as for distinguishing key pattern representations related to goal-directed behavior over different stages of a task (Hubbard et al.,

2019). This literature underpins the rich potential of the decoding approach to classify time-resolved task information encoded in the EEG signal.

The preparation and running of all four experiments took place in designated venues in the School of Psychology of Bangor University, following ethics approval by the School's Research Ethics Committee. Specifically, the entire preparatory work (e.g., setup of technical equipment, programming), the training/test sessions for *experiments 1-3*, and the training/test behavioral sessions for *experiment 4* were delivered at the Skilled Action & Memory Lab. The Psychology Open-access Electrophysiology and Topographic (POET) Lab hosted the EEG session for *experiment 4*, including prior laboratory work required for preparing the system for data acquisition.

For the implementation of all four experiments, a total of 102 participants were recruited. From this cohort, the datasets of 73 participants (corresponding to circa 377.1 h of data collection) were fully analyzed after excluding pilot, noisy or incomplete datasets due to withdrawal as well as data from participants showing outlier performance (*cf.* Chapter 2).

1.4.2 Scope and delimitations

Based on the aims and objectives outlined above and the time constraints that this research project had to adhere to, its primary scope was to identify and establish the behavioral and neural signature of a sequence planning mechanism, focusing on order and timing, in the healthy brain. At this early stage of the present line of research, it is necessary to first establish the workings and functional role of the planning mechanism under investigation before moving on to examine any defective functioning in populations with movement disorders. Therefore, for the conduction of all studies, only healthy, non-expert (i.e., with no professional experience in motor skilled sequencing) participants were recruited for data collection. In addition, the effects of hand dominance in motor sequence planning are poorly studied. Limited evidence suggests that left and right handers do not exhibit differences in motor planning during an action selection task (Sadeghi et al., 2021) whilst the left hemisphere engagement of the premotor-parietal network during sequence planning and execution occurs independently of hand dominance (Serrien & Sovijärvi-Spapé, 2015). However, to the best of our knowledge, there are no available data on handedness effects specifically on the control of order and timing, thus for the present studies only right-handed participants were recruited.

Although this research largely draws on findings from neural network studies - CQ and RNNs - it did not seek to investigate a parallel *vs* serial processing hypothesis, respectively. Instead, the outlined questions are clearly set under the CQ hypothesis, formulating alternative hypotheses where applicable according to conclusions drawn from the relevant literature. Finally, studying the planning of well-learnt sequences inevitably intersects with topics of motor skill learning, WM, LTM, motor memory, and memory consolidation. However, delving into the mechanisms of each of these domains was beyond the scope of this thesis.

1.4.3 Significance

The time before we execute a skilled movement sequence contains valuable information about the spatiotemporal profile of the upcoming action. The goal of this research is to advance our knowledge of motor sequence planning by shedding light on the preparatory mechanisms of serial order and timing control. Identifying a behavioral marker of sequence planning and its relation to subsequent performance may pave the way for establishing a widely accessed and cost-efficient behavioral tool for assessing preparatory movement organization. Additionally, the findings on the underpinnings of neural modulation of sequence speed in association with serial order during planning will benefit clinical populations who exhibit disruptive timing during motor sequence execution.

1.4.4 Chapter scheme

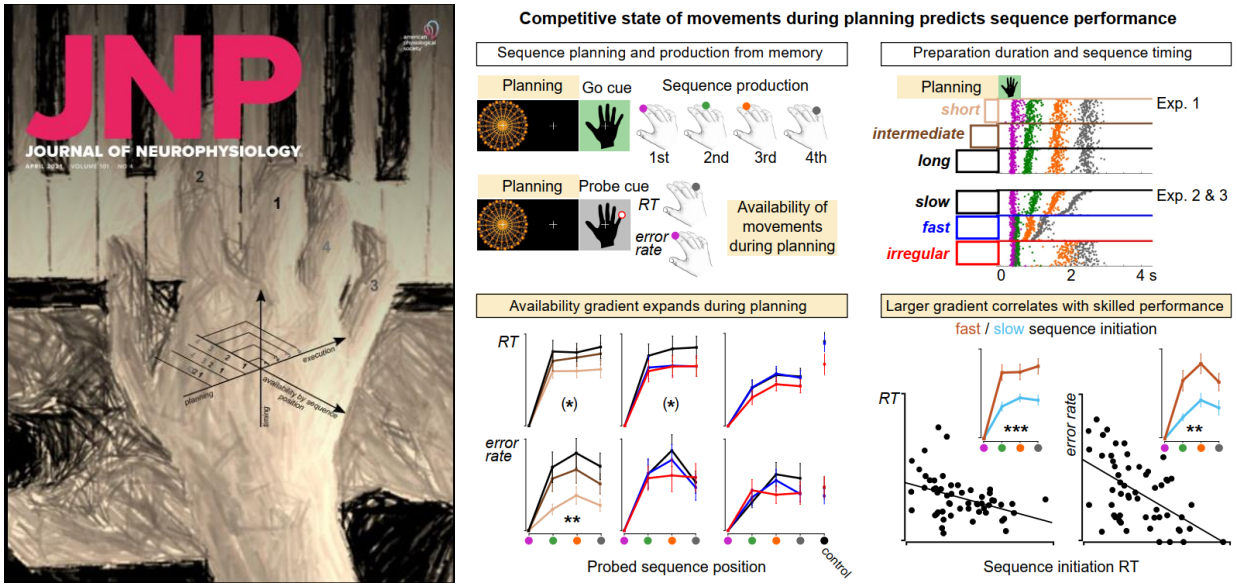
Following a historical backdrop and a thorough, critical evaluation of the up-to-date literature discussed in the current Chapter, the subsequent Chapters present the empirical work conducted for addressing the above outlined research questions. Specifically, Chapter 2 comprises *experiments 1-3* and Chapter 3, *experiment 4*. Finally, Chapter 4 discusses the present findings in relation to current knowledge and concludes all together on the significance of this work.

Chapter 2

Competitive state of movements during planning predicts sequence performance - Experiments 1, 2 and 3

This Chapter contains identical parts from a peer-reviewed article published in the Journal of Neurophysiology (JNP) (Mantziara, Ivanov, Houghton & Kornysheva, 2021) and featured in the JNP April – June 2021 complementary cover (see below cover and graphical abstract). Here, the JNP article has been slightly modified only to meet the formatting requirements of this thesis.

Mantziara, M., Ivanov, T., Houghton, G., & Kornysheva, K. (2021). Competitive state of movements during planning predicts sequence performance. *Journal of Neurophysiology*, *125*(4), 1251-1268. https://doi.org/10.1152/jn.00645.2020 "Copyright (2021) by the American Physiological Society."



2.1 Abstract

Humans can learn and produce skilled movement sequences from memory, yet the nature of sequence planning is not well understood. Previous computational and neurophysiological work suggests that movements in a sequence are planned as parallel graded activations and selected for output through competition. However, the relevance of this planning pattern to sequence production fluency and accuracy, as opposed to the temporal structure of sequences, is unclear. To resolve this question, we assessed the relative availability of constituent movements behaviorally during the preparation of motor sequences from memory. In three separate multisession experiments, healthy participants were trained to retrieve and produce four-element finger press sequences with particular timing according to an abstract sequence cue. We evaluated RT and error rate as markers of movement availability to constituent movement probes. Our results demonstrate that longer preparation time produces more pronounced differences in availability between adjacent sequence elements, whereas no effect was found for sequence speed or temporal grouping. Further, participants with larger position-dependent differences in movement availability tended to initiate correct sequences faster and with a higher temporal accuracy. Our results suggest that competitive preactivation is established gradually during sequence planning and predicts sequence skill, rather than the temporal structure of the motor sequence.

2.2 New & Noteworthy

Sequence planning is an integral part of motor sequence control. Here, we demonstrate that the competitive state of sequential movements during sequence planning can be read out behaviorally through movement probes. We show that position-dependent differences in movement availability during planning reflect sequence preparedness and skill but not the timing of the planned sequence. Behavioral access to the preparatory state of movements may serve as a marker of sequence planning capacity.

Keywords: *Competitive queuing; Error rate; Motor planning; Reaction time; Sequence control*

2.3 Introduction

Producing movement sequences from memory fluently is an essential capacity of primates, in particular humans. It enables a skilled and flexible interaction with the world for a range of everyday activities - from tool use, speech, and gestural communication to sports and music. Key to fluent sequence production is sequence planning before the initiation of the first movement (Lashley, 1951; Rosenbaum, 1985), with longer preparation time benefitting sequence execution, i.e., reducing initiation time after a *Go* cue and improving accuracy (Ariani & Diedrichsen, 2019). However, the underlying nature and content of sequence planning is still debated (Remington, Egger, et al., 2018).

Different computational accounts of sequence control make contrasting predictions with regard to the content of sequence planning. Models postulating a purely serial control of motor sequences suggest that a well-learnt sequence is a cohesive entity, rather than a series of individual movements, e.g., individual strokes when drawing a geometrical figure or finger presses playing the piano (Goudar & Buonomano, 2018; Laje & Buonomano, 2013). They predict that sequence planning activity reflects bringing the neural trajectory toward the correct neural state of sequence initiation from which it cascades serially through a learnt trajectory. Sequence planning would therefore entail the preparation of the state occupied by the first movement, e.g., using a null state to allow preparation without premature initiation, as shown empirically for reaching movements (Kaufman et al., 2014; O'Shea & Shenoy, 2016). By contrast, models postulating parallel sequence control, such as CQ models (Houghton, 1990), propose simultaneous control of the items, here movements, in a sequence. They predict that preparatory neural activity preactivates sequence movements concurrently. Specifically, the neural activation pattern for each movement is weighted according to its temporal position in the respective sequence (Burgess & Hitch, 1999; Hartley & Houghton, 1996), resulting in a position-dependent preactivation gradient for each upcoming movement in the sequence. Indirect support for parallel and independent neural control of sequential movements stems from observations of serial recall including transposition of neighbouring sequence items and items occupying the same position in different chunks (Glasspool & Houghton, 2005; Hartley & Houghton, 1996; Henson, 1998b), and excitability of forthcoming movements during sequence production (Behmer et al., 2018). Direct neurophysiological support for the parallel control of sequence movements has been provided in the context of well-trained finger se-

quences (Kornysheva et al., 2019; Pinet et al., 2019), saccades (Basu & Murthy, 2020), and drawing of geometrical shapes (Averbeck et al., 2002). Specifically, during planning, the probability of neural patterns associated with each movement in the sequence was highest for the first and lowest for the fourth and fifth movements of the planned sequence. This effect could not be explained by a graded prepressing of the corresponding fingers according to their order and was observed at the trial-by-trial level, suggesting that this competitive preactivation is not an artefact of trial averaging (Kornysheva et al., 2019). Importantly, the ordered preactivation gradient of sequence movements during planning was relevant to subsequent execution. In particular, the quality and strength of this gradient was predictive of sequence production accuracy such that participants with stronger preactivation differences between the sequence items during planning were more accurate during sequence production. Together, these data suggest that skilled sequence production involves an orderly parallel planning of several movements in advance before sequence initiation and predicts better sequence performance.

Although the preactivation gradient during planning has been shown to predict subsequent execution, it remains unclear what this preparatory pattern reflects—the skill of sequence production (fluency of initiation and accuracy of the sequence execution) or the temporal structure of the sequence (speed and temporal grouping). Most CQ models assume the presence of a temporal or positional context layer and that the activity gradients are learned by associations of the latter to each sequence item in the parallel planning layer, e.g., through Hebbian learning (Burgess & Hitch, 1999). The form of activity in the context layer can be as simple as a decaying start signal (Page & Norris, 1998), a combination of start and end signals (Houghton, 1990, 2018), or a sequence of overlapping states (Burgess & Hitch, 2006; Houghton, 1990). Although primarily encoding serial order of sequence items, models utilizing overlapping states can implement effects of temporal grouping or sequence rhythm (Hartley et al., 2016; Houghton, 1990), making timing an intrinsic property of the CQ of sequential movements. Likewise, a separate timing process (Kornysheva et al., 2013; Kornysheva & Diedrichsen, 2014; Medina et al., 2005; Spencer et al., 2009; Ullén & Bengtsson, 2003; Zeid & Bullock, 2019) may modulate the parallel planning of the serial order of items, e.g., in the parallel planning layer. In both cases, the competitive preactivation gradient of movements during planning would reflect the temporal grouping or temporal proximity of movements in the upcoming sequence, with movements closer together in time having more similar levels of preactivation than those that are further apart (Houghton, 1990). By contrast, sequence

timing may not impact the competitive preactivation of sequential movements during planning and interact with the latter during execution only.

To investigate the nature of sequence planning and its relation to subsequent execution, we developed a behavioral paradigm to capture the preparatory state of each constituent movement of a well-learnt sequence during planning. Following training, participants prepared a motor sequence from memory following an abstract visual stimulus associated with a particular sequence of finger presses performed with a particular speed or temporal grouping. In half of the trials during the test phase, the *Go* cue was replaced by a finger press cue prompting the production of movements associated with different positions in the sequence. We used behavioral availability for fast and correct execution of the presses in these *Probe* trials (RT and error rate) as behavioral markers of the relative preactivation of upcoming movements during sequence planning.

We hypothesized that if CQ during planning primarily reflected the accuracy of the sequence plan (Averbeck et al., 2002; Kornysheva et al., 2019), but not its timing, we would predict a gradual differentiation of the position-dependent preactivation gradient with longer sequence preparation time. Accordingly, we would observe an increase of position-dependent differences in press availability across preparation durations of 500, 1000, and 1500 ms, despite matched speed and temporal grouping of sequence production. Further, participants with a more pronounced gradient would be more fluent and accurate, specifically show more rapid sequence initiation of correct sequences after the *Go* cue, more accurate timing, and fewer finger press errors.

Alternatively, if the gradient reflected the timing of the sequence during planning, movements planned to be executed closer in time would show smaller position-dependent differences relative to movements further apart. Accordingly, sequences twice as fast (speed manipulation) would result in more similar levels of availability of movements in neighboring sequence positions. Further, the latter would be modulated by irregular IPIs with shorter versus longer IPIs being accompanied by smaller versus larger differences in position-dependent availability during planning, respectively (temporal grouping manipulation).

We report that during the 1.5 s of sequence retrieval and preparation from memory, the behavioral availability of sequential movements decreases on average with their planned serial position, up to the last but one. Specifically, movement probes associated with later sequence positions were progressively more likely to lead to erroneous presses during planning, and correct

presses were executed more slowly. This characteristic preparatory gradient of movement availability increased with preparation duration rendering movements preplanned to occur in later compared with earlier sequence positions progressively less available. Across participants, the size of this gradient during preparation correlated with more fluent initiation and temporally accurate sequence production. Contrary to the timing hypothesis, we found no reliable effect of sequence speed or temporal grouping on movement availability during planning. Based on these data, we propose that sequence planning involves a competitive preactivation gradient of sequential movements during sequence planning, which operates independently of sequence timing and facilitates skilled sequence performance.

2.4 Materials and Methods

2.4.1 Participants

Data were collected from a total of 55 right-handed University students (*experiment 1*: N = 19, 11 females; M = 24.2 years, SD = 4.1; *experiment 2*: N = 18, 11 females; M = 24.2 years, SD = 4.5; *experiment 3*: N = 18, 9 females; M = 20.8 years, SD = 2.4). Four additional participants were tested but excluded from analysis based on their sequence production finger error rate (*cf.* Participant Exclusion Criteria). They were hypothesis-naive and had no previous exposure in performing a similar experimental task. All participants had normal or corrected-to-normal vision and reported no history of neurological or psychiatric disorders or hearing problems. Handedness was evaluated through the online Handedness Questionnaire (http://www.brainmapping.org/shared/Edinburgh.php) adapted from the Edinburgh Handedness Inventory (Oldfield, 1971) (*experiment 1*, M = 88.4, SD = 9.4; *experiment 2*, M = 90.6, SD = 9.7; *experiment 3*, M = 90, SD = 11.8). All participants provided written informed consent before participation and were debriefed after completing the study. They were compensated either monetarily or with course credits at the end of the experiment. All procedures were approved by the Bangor University School of Psychology Research Ethics Committee (Ethics Review Board Approval Code 2017-16100-A14320).

2.4.2 Apparatus

For all three experiments, participants were seated in a quiet room in front of a 19-inch LCD monitor (LG Flatron L1953HR, 1280 × 1024 pixels), wearing headphones for noise isolation. All instructions, visual stimuli, and feedback were precisely timed by the monitor's refresh rate (60 Hz) and controlled by Cogent 2000 (v1.29) (http://www.vislab.ucl.ac.uk/cogent.php) through a custom-written MATLAB program (v9.2 R2017a, The MathWorks, Inc., Natick, MA). In *experiments 1* and *2*, a Pyka 5-button fiber optic device (Current Designs) was used to record the responses. A customized foam channel stabilized the cable and a thin anti slip mat, placed underneath the response device, prevented from sliding during the task. The response device was positioned horizontally and adjusted for each participant to ensure good control over the target buttons as well as arm and wrist comfort. Participants were instructed to place the right index, middle, ring, and little fingers on the respective target buttons of the device. *Experiment 3* used an identical experimental setup with the exception that responses were recorded using a computer keyboard. Here, participants were instructed to place their right thumb in addition to the rest of the right-hand fingers on the designated keyboard keys. For hand stabilization and comfort, their wrist was positioned on a rest cushion.

2.4.3 Experimental design

All three experiments employed a visually cued motor learning task adapted from Kornysheva et al. (2019). *Experiments 1* and *2* involved the recording of sequential and single button presses produced with the four fingers (index, middle, ring, and little) of the right hand. *Experiment 3* additionally required single presses with the thumb. In all experiments, participants were trained to associate a visual cue (an abstract fractal shape, henceforth *Sequence* cue) with a four-element finger sequence produced with a specific timing. The paradigm employed two main trial types: *Sequence* and *Probe* (single press) trials. *Sequence* trials were further divided into visually instructed and memory-guided trials. Instructed *Sequence* trials involved the presentation of four visual digit cues (index, middle, ring, and little) at specified intervals comprising a unique target sequence. These were only used during training in the first two days, and during two refresher blocks on the third day (Figure 2.1a). The test phase on the third day involved sequence production without visual guidance (Figure 2.1b). *Probe* trials involved the production of only one

visual digit cue (*Probe* cue) corresponding to one of the serial positions in the target sequence (Figure 2.1c).

Experiment 1 - preparation duration. All participants were trained to produce two different finger sequences comprising four presses with target IPIs of 800 ms (slow timing). Two additional sequences served as practice sequences to impose familiarization with the task. All sequences were randomly generated offline for each participant through a custom-written MATLAB code. The sequence generation process excluded sequences with ascending and descending digit triplets and identical finger positions.

All trial types started with a *Sequence* cue. The *Sequence* cue had a fixed duration of 400ms followed by a fixation cross, the latency of which varied depending on the delay period between the *Sequence* cue and *Go* cue onsets. The resultant short (500 ms), intermediate (1000 ms), and long (1500 ms) delay periods comprised the three preparation duration conditions employed in the task. After the delay period, a black right-hand stimulus appeared as the *Go* cue.

In an instructed *Sequence* trial, the *Go* cue was presented on a gray background for 2400 ms. A white circle appeared on top of the corresponding finger digits of the hand stimulus sequentially to guide the participants throughout the execution of the sequence. The time intervals between the digit cues formed the target timing of the sequence and defined its duration of 2400 ms. To achieve finger and temporal accuracy during training, participants were asked to 'synchronize' the correct finger presses with the digit cues until the completion of the sequence. As the first digit cue of a sequence appeared at the same time as the *Go* cue, immediate initiation of the sequence was emphasized in the instructions. In a memory-guided *Sequence* trial, the *Go* cue was presented on a green background, remaining on the screen for 2400 ms. Memory-guided *Sequence* trials were devoid of finger digit cues, requiring participants to produce the upcoming target sequence from memory. Participants were instructed to initiate the sequence as quickly as possible and produce the sequence according to its target finger order and timing. In a *Probe* trial, after the delay period, the *Go* cue was replaced with a *Probe* cue, namely, a single digit cue, displayed for 1000 ms. The *Probe* cue prompted a single press with a corresponding finger as fast and accurately as possible. Participants were encouraged to avoid premature responses (before the *Go* cue) in all trial types. Following the *Go* cue in any trial type, a fixation cross (1000 ms) and, subsequently, feedback (1000 ms) were presented on the screen. The duration of a *Sequence* trial was 5.4 s, and a *Probe* trial had a duration of 4 s, including feedback. The inter-trial interval (ITI) was fixed at 800 ms.

The experiment consisted of two 90-min-long training sessions (days 1 and 2) and a test session (day 3), which took place over three consecutive days. Day 1 commenced with a practice block, which involved two instructed and two memory-guided *Sequence* trials for each of the target sequences, and two randomly selected *Probe* trials, with randomly chosen preparation durations. Over the three days, participants serially underwent a pre-training (2 blocks), a training (36 blocks), a post-training (2 blocks), and a test phase (2 refresher training blocks and 16 test blocks), completing a total of 58 blocks. To assess sequence planning and execution from memory, only data from the test phase are presented here.

Participants were naïve as to the structure of the transition from the training through to the test phase and which block type they were administered (Figure 2.1a). The training phase was organized in three stages: 12 blocks of 288 instructed *Sequence* and 72 *Probe* trials (stage A, 80 % instructed *Sequence* and 20 % *Probe* trials in each block), 12 blocks of 144 instructed, 144 memory-guided *Sequence* and 72 *Probe* trials (stage B, 40 % for each *Sequence* type and 20 % *Probe* trials in each block), and 12 blocks of 288 memory-guided *Sequence* and 72 *Probe* trials (stage C, 80 % memory-guided *Sequence* and 20 % *Probe* trials in each block). Each training block (3 min long) consisted of 30 trials. On each training block, there was a 20 % occurrence of *Probe* trials (6 in each block) comprising a total of 216 throughout the training blocks. All *Probe* trial conditions (24; 2 sequences 3 preparation durations 4 digits) were counterbalanced across the training blocks. The test phase (day 3) started with two refresher training blocks (stage B, 40 % for each Sequence type and 20 % *Probe* trials in each block) and immediately progressed to 16 blocks of 48 trials each, in which 24 memory-guided *Sequence* and 24 *Probe* trials were randomly presented (test, 50 % memory-guided *Sequence* and 50 % *Probe* trials). Duration of each test block was 4.4min.

The preparation duration conditions were counterbalanced across the two target sequences in memory-guided *Sequence* and *Probe* trials in each block. This resulted in a total of 128 memory-guided *Sequence* trials per preparation duration condition, across blocks. In *Probe* trials, each *Probe* cue was combined with the three preparation duration conditions resulting in 32 trials per digit cue per preparation duration condition. The test phase had a total of 768 trials (384 memory-guided *Sequence* and 384 *Probe* trials). Overall, the participants underwent 2004 trials excluding the practice trials.

Preparation duration (foreperiod) effects on RT have been associated with carry-over effects from preceding to current trials and may bias our RT findings if trial history is unbalanced (Langner et al., 2018; Steinborn & Langner, 2012). Post hoc, we examined the preparation duration conditions in both *Probe* trials and memory-guided *Sequence* trials (*cf.* Supplemental Figure S1, a and b; see https://doi.org/10.6084/m9.figshare.13688131 or / Supplemental Figure A.S1 in Appendix A). The mean preparation duration of preceding trials (previous, *n-1*, or two trials previously, *n-2*) did not vary depending on the serial position associated with the target sequence in any of the preparation durations of a current trial (*n*) [4 x 3 repeated measures ANOVAs: Position x Preparation duration *n-1*, $F(6, 108) = 0.88$, $p = .511$, $\eta^2p = .05$; Position x Preparation duration *n-2*, $F(6, 108) = 1.14$, $p = .344$, $\eta^2p = .06$]. Equally, analysis of the sequence production trials revealed that preparation duration of a current trial did not vary with the mean preparation duration of preceding trials [one-way repeated measures ANOVAs: Preparation duration *n-1*, $F(2, 36) = 2.53$, $p = .093$, $\eta^2p = .12$; Preparation duration *n-2*, $F(2, 36) = 0.36$, $p = .701$, $\eta^2p = .02$]. This demonstrates a balanced design in which the foreperiod length history up to two previous trials was unlikely to bias RT or error rates on the current trial.

Experiment 2 - sequence timing. Procedures for *experiment 2* were identical to *experiment 1* except that the delay period was fixed at 1500 ms and participants were trained in associating three target sequences. Each featured a unique *Sequence* cue associated with one finger order instructed to be performed at three target IPIs: slow (800–800–800 ms), fast (400–400–400 ms), and irregular (400–1600–400 ms), comprising the three timing conditions. The timing manipulation was used to test the effect of temporal proximity and grouping on the preactivation of movements during preparation. The relative compression and expansion of target IPIs by a scaling factor of 2 in the fast and irregular timing conditions relative to the baseline condition (long preparation duration and slow timing conditions) is in line with previous work on motor timing (J. Wang et al., 2018). Although participants were trained to produce specific IPI durations imposed by the target IPIs, relative timing, i.e., temporal IPI modulations relative to the baseline condition, was key to evaluating the influence of timing at the group and individual levels. Thus, relative timing was calculated offline from memory-guided *Sequence* trials (test phase) as each IPI duration (1st, 2nd, 3rd) relative to the mean produced IPI duration in the baseline condition (in percent). Accordingly, relative temporal error was defined as the mean absolute deviation from the target IPI per trial in percent.

In a *Sequence* trial, the *Go* cue remained on the screen for 3000 ms, whereas in a *Probe* trial, the *Probe* cue for 1000 ms. This was followed by a fixation cross (1000 ms) and feedback (1000 ms) with a varying ITI of 500, 900, and 1300 ms. As a result, a *Sequence* trial was 6.5 min long and a *Probe* trial 4.5 min long. The participants underwent the same structure of training and test sessions as in *experiment 1*. The timing conditions were equally matched to the number of all trial types in each block. Overall, in this experiment participants completed 2016 trials over 58 blocks.

Experiment 3 - sequence timing and control movement. Procedures for *experiment 3* were identical to *experiment 1*, except the introduction of additional *Probe* trials that cued the thumb. Thumb presses were not part of any target finger sequence. Thus, they served as a control condition to obtain RTs and error rates for unplanned movements. Across each training stage, there were 60 *Probe* trials, whereas the test phase (30 blocks 26 trials) contained 360 memory-guided *Sequence* trials (120 trials per timing condition), 360 *Probe* trials (30 trials per digit per timing condition), and 60 thumb *Probe* trials (20 trials per timing condition). Overall, participants completed 1990 trials over 72 blocks, excluding the practice block.

Feedback. In all experiments, a points system was designed to reward fast initiation and accurate performance and avoid any performance drift in blocks with motor production from memory. To incentivize the participants to gain as many points as possible on each trial, we offered an extra monetary reward (£10) to those two with the highest total points. In *Sequence* trials, points (0–10) could be awarded based on three performance criteria: finger press accuracy, sequence initiation RT, i.e., response from *Go* cue to the first press, and temporal error (deviation from the target IPIs). Points in each *Sequence* trial were the sum of the points for initiation RT and mean temporal error, multiplied by finger press accuracy points (0 or 1). If at least one incorrect press or an incorrect number of presses was recorded (< 4 or > 4), 0 points were given on that trial, regardless of initiation RT and temporal error. Points gained from the initiation RT component of the sequence were defined by tolerance RT windows of 0–200, 200–360, 360–480, 480–560, and 560–600 ms resulting in 5, 4, 3, 2, and 1 points, respectively. For late (> 600) responses, 0 points were given. Mean temporal error was calculated for each trial as deviation of presses from target timing in percent of the respective target IPI to account for the scalar variability of timing (Jazayeri & Shadlen, 2010; Rakitin et al., 1998). Thresholds for mean absolute percentage deviation across

all correct presses were set at 10, 20, 30, 40, and 50 % assigning 5, 4, 3, 2, and 1 points, respectively. Mean temporal error above 50 % resulted in 0 points.

Points (0–5) in each *Probe* trial were calculated based on finger press accuracy (0 or 1) and RT utilizing the same tolerance RT windows. In the case of an incorrect press or incorrect number of presses (< 1 or > 1), 0 points were given regardless of the RT length. The points were displayed on the screen after each *Probe* trial, whereas after a *Sequence* trial they were presented above a schematic visual feedback.

Schematic feedback provided information on both finger press accuracy and temporal error performance only after each *Sequence* trial. An ‘x’ or a ‘-’ symbol was shown for every correct or incorrect press, respectively. For early presses, the respective symbol was displayed below the midline (target timing), whereas for late presses it was displayed above. For orientation, the lines above and below (upper and lower border) corresponded to timing deviations as large as the target IPI itself (100 %). Timing deviation was only shown for second, third, and fourth presses of the sequence. The first symbol reflected the first press and was always positioned on the midline, representing the starting point of the sequence. Participants were instructed to adjust their performance by keeping the ‘x’ symbols as close to the midline as possible. Deviation from the target onset (presented or assumed) rather than the interval timing encouraged participants to synchronize with the instructed sequences during training, however, may have contributed to a tendency to compress the overall sequence length during the memory-guided *Sequence* trials.

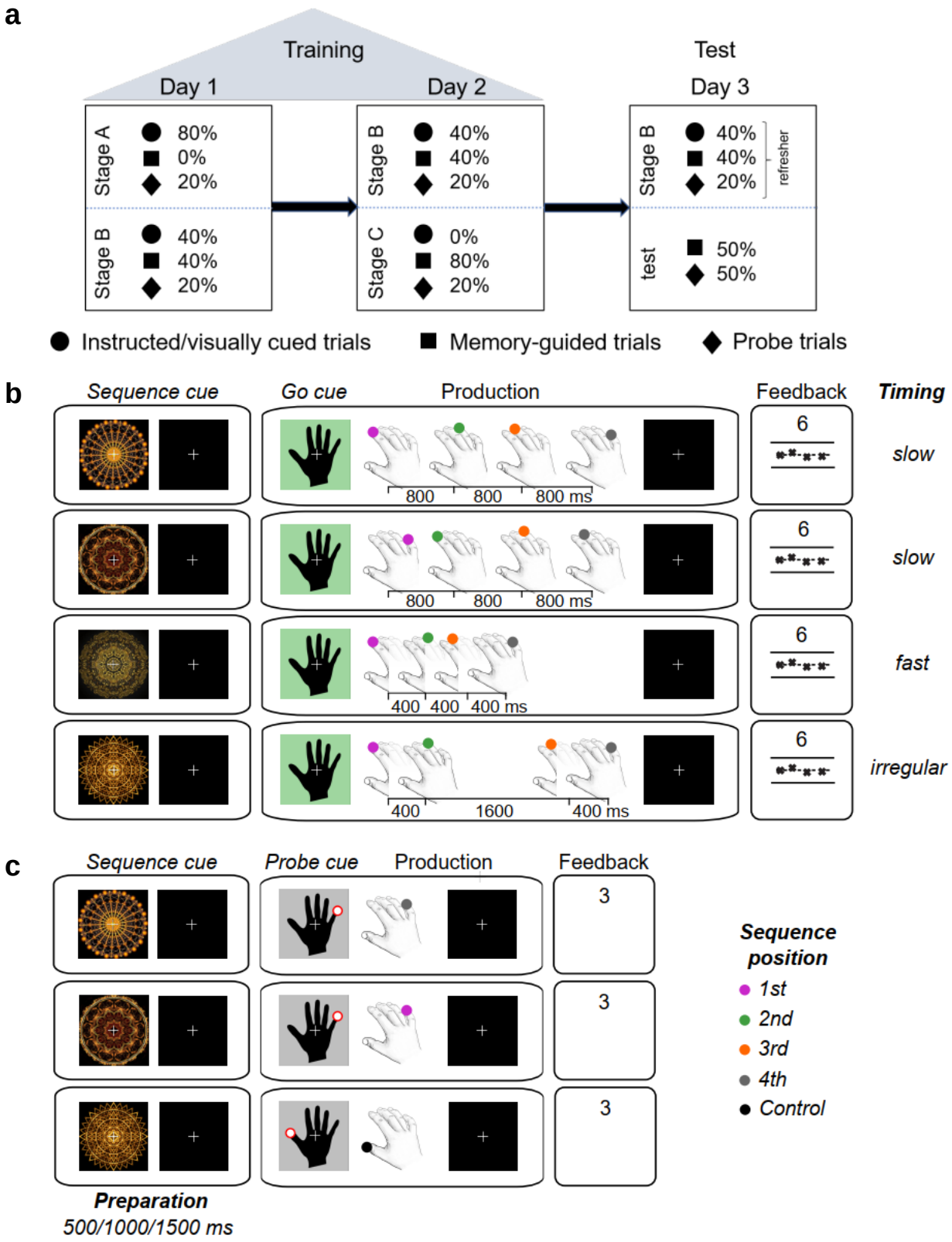


Figure 2.1 | Design and experimental conditions. a. The first two days integrated the three training stages. Participants progressed from entirely instructed sequence production trials (stage A) to blocks of mixed trials (stage

B) and, finally, to producing the target sequences from memory during the last stage of the training (stage C). All training stages incorporated a fixed percentage of *Probe* trials, randomized in each block, to ensure a degree of familiarity with single-press *Probe* cues. In the test phase (day 3), participants underwent two refresher blocks (stage B) and, subsequently, an equal number of memory- guided *Sequence* trials and *Probe* trials (test). **b.** Test phase: After training, participants were prompted to produce four-element finger sequences from memory following a *Go* cue. Each finger order or timing corresponded to a unique abstract visual *Sequence* cue presented for up to 1500ms before the *Go* cue (preparation period). *Experiment 1* cued the production of sequences with two different finger orders and isochronous timing (slow). Here, we manipulated the duration of the preparation period (500, 1000, 1500 ms). In *experiments 2* and *3*, the *Sequence* cues had a fixed preparation duration of 1500 ms and prompted the production of sequences with the same finger order but a different timing (slow, fast, irregular). In all three experiments, the target IPIs, illustrated in ms, were used to train participants to develop a relative timing proportionate to the target timing. Participants received visual feedback in each trial on the accuracy of the finger order and their timing. Points were based on finger press accuracy, initiation RT, and temporal accuracy (*cf.* Materials and Methods). **c.** Test phase: In all experiments, we introduced *Probe* trials, in which, following the preparation period, the Go cue was replaced with a *Probe* cue. That prompted a particular finger digit to be pressed, corresponding to each sequence position or a control movement, which did not feature in any sequence production. The *Probe* condition was used to obtain the RT and error rate for each position at the end of the preparation period. The participants received points for accurate presses and fast RTs. RT, reaction time; IPIs, inter-press intervals.

2.4.4 Participant exclusion criteria

In each experiment, mean finger error rate (percent error trials out of total trials) during sequence production from memory (memory-guided *Sequence* trials; test phase) above three standard deviations of the group mean performance was considered as outlier performance. This was to ensure that participants reached a comparable skill level in sequence production. Additionally, it allowed for a sufficient number of trials for RT analysis per participant, which included correct trials only. Data exclusion was blind to the individual *Probe* trial performance and, thus, independent of the measures analyzed to test our hypotheses. In *experiment 1*, the data of one participant were excluded who showed 53.1 % finger error in the short, 54.7 % in the intermediate, and 53.9 % in the long preparation duration conditions. Two participants' data sets were removed from *experiment 2*, one with 25 % finger error in the slow timing and 18.8 % in the irregular timing conditions, while the other showed 44.5 % finger error in the fast timing condition. The data of one participant were excluded from *experiment 3* due to 12.5 % finger error in the fast timing condition. Overall, the data of 19 participants were analyzed for *experiment 1*, 18 participants for *experiment 2*, and 18 participants for *experiment 3*.

2.4.5 Data analysis

Data analyses were performed using custom written code in MATLAB (v9.2 R2017a, The MathWorks, Inc., Natick, MA) and SPSS v22.0 (IBM Corp., Armonk, NY).

Sequence planning. Median RT (correct trials only) and mean error rate in *Probe* trials were used as dependent measures for assessing the availability of movements corresponding to different sequence positions during planning. First, we tested for the RT and error rate increases from 1st to 2nd, 2nd to 3rd, and 3rd to 4th positions in each experiment. These were tested in the baseline condition common across the three experiments (long preparation duration and slow timing conditions). One-tailed paired samples *t* tests were performed on the raw RTs and error rates, based on the one - sided hypothesis of an increase with position number. The position-dependent differences for error were further examined in the lower and upper RT quartiles to test for position - dependent increases of press error depending on response speed.

Second, to test for the interaction of factors Position (1st, 2nd, 3rd, 4th) and Preparation Duration (short/500 ms, intermediate/1000 ms, long/1500 ms) in *Probe* trials of *experiment 1*, the raw RTs and error rates were submitted to two-way repeated measures ANOVAs. Using the same test, we assessed the interaction of the factors Position and Sequence Timing (slow, fast, irregular) in *experiments 2* and *3*. Significant interaction effects were investigated using planned repeated contrasts to determine the changes relative to baseline that were driving the interaction. To evaluate the RT and error rate for the control movement (*experiment 3*), we used two-tailed paired samples *t* tests (control *vs* 4th position).

Third, we calculated the increase of RT and error rate for each probed position relative to the first position in each condition (in %) for each participant. This enabled us to quantify and visualize the relative position-dependent increases in each condition (Figure 2.2). Further, we calculated the average relative RT and error differences between adjacent positions (mean difference across 1st minus 2nd, 2nd minus 3rd, 3rd minus 4th) in the baseline condition for each participant as markers of the movements' preactivation gradient size during sequence planning. One-way repeated measures ANOVAs in each experiment were used to assess modulations of the latter by the experimental conditions (Preparation Duration in *experiment 1* and Timing in *experiments 2* and *3*). To test for the association between these measures and sequence performance (initiation RT of correct sequences, relative temporal error, and finger error rate), six one-tailed Pearson's correlation analyses were performed across experiments ($N = 55$). Further, a median split was calculated

based on each performance measure for raw mean RTs and error rates for each position in the baseline condition. These were subjected to three mixed ANOVAs (Position x Group) to test for the position-dependent differences in movement availability during planning depending on performance (N = 55).

Finally, we looked at the percent of presses associated with the 1st, 2nd, 3rd, and 4th positions of the planned sequence in erroneous *Probe* trials, for each probed position separately (four one - way repeated measures ANOVAs; N = 55).

Sequence production. Only the memory-guided *Sequence* trials (test phase) were used for analyzing the components of sequence production. First, relative timing (percent duration of each IPI relative to the mean produced IPI in the baseline condition) was subjected to a 3 x 3 repeated measures ANOVA, for each experiment, depending on IPI (1st, 2nd, 3rd) and Preparation Duration (*experiment 1*) or Sequence Timing (*experiments 2* and *3*). Finally, to evaluate the fluency and accuracy of sequence production, we calculated sequence initiation RT (online recording of *Go* cue to first press latency), relative temporal error (deviation from target IPI), and finger press error (percent trials with incorrect presses). These constituted the three performance measures to reflect skill in sequence execution and were analyzed for each experiment separately in nine one-way repeated measures ANOVAs to assess modulations of skill by Preparation Duration or Timing.

The error data of both *Probe* and *Sequence* trials were arcsine transformed (Winer et al., 1991) before they were submitted to the ANOVA models and *t* tests due to violation of normality. Partial eta-squared ratios and Cohen's *d* are reported as measures of effect sizes in the corresponding tests.

2.5 Results

2.5.1 Availability of movements during sequence planning is dependent on their position in the planned sequence

In all three experiments, participants were trained for 2 days to associate abstract visual cues with four-element finger sequences. They were instructed to produce the sequences with a particular temporal structure (Timing: slow, fast, irregular) following a brief preparation period (Preparation Duration: short/500 ms, intermediate/1000 ms, long/1500 ms). In half of the trials in the test phase (day 3), a *Probe* cue instructed participants to respond with the corresponding finger

press as quickly and accurately as possible at the end of the planning phase (Figure 2.1c). This allowed us to probe the availability of movement associated with each position of the planned sequence (1st–4th) for accurate and fast execution. Based on our previous neurophysiological findings (Kornysheva et al., 2019) in a similar task that showed a graded preactivation of movements during planning according to their sequential position, we hypothesized that the behavioral availability of movements during planning will be position dependent. Specifically, we predicted a significant increase in RT and error rate for probed movements from 1st to 2nd and 2nd to 3rd positions. Based on our neurophysiological results, we did not expect an increase in movement availability from penultimate to final position (here: 3rd to 4th), but the latter has been previously observed in the context of a drawing sequence task in nonhuman primates (Averbeck et al., 2002). Additionally, we included probes for a control movement (*experiment 3*) to reveal whether the movement associated with the last position of the planned sequence is more accurately and quickly selected and executed than a movement that is not part of the sequence. A higher behavioral availability of the last position movement would suggest that the sequence movements are more preactivated, albeit to a different level, rather than activated and inhibited relative to a baseline movement. Position-dependent RT and press error increases were analyzed from trials in the experimental condition, which constituted the baseline in all three experiments (long preparation duration - 1500 ms - and slow timings).

Reaction times to movement probes. Figure 2.2a shows the percent RT increase relative to the RT for the movements associated with the first position, respectively [*cf.* Supplemental Figure S2a for raw RT values (see https://doi.org/10.6084/m9.figshare.13227953 or Supplemental Figure A.S2a in Appendix A); Supplemental Table S1A for statistics (see https://doi.org/10.6084/m9.figshare.13673605 or Supplemental Table A.S1a in Appendix A)]. *Experiment 1* revealed a significant RT increase from 1st to 2nd position [paired samples *t* test: $t(18) = -7.45$, $p < .001$, $d = 1.32$, one-tailed] but not from 2nd to 3rd position [$t(18) = 0.05$, $p = .479$, $d = 0.01$] or from 3rd to 4th position [$t(18) = -0.72$, $p = .241$, $d = 0.09$]. *Experiment 2* replicated the RT results from *experiment 1*, revealing a significant RT increase from 1st to 2nd position [$t(17) = -6.45$, $p < .001$, $d = 1.60$], but not from 2nd to 3rd [$t(17) = -0.63$, $p = .267$, $d = 0.16$] or 3rd to 4th position [$t(17) = -0.25$, $p = .404$, $d = 0.05$]. *Experiment 3* showed a significant RT increase from 1st to 2nd position [$t(17) = -4.61$, $p < .001$, $d = 1.03$] and, unlike the *experiments 1* and *2*, also from 2nd to 3rd position [$t(17) = -2.41$, $p = .014$, $d = 0.40$]. As in experiments 1 and 2, the RT

increase from 3rd to 4th position was not significant [$t(17) = -0.21$, $p = .417$, $d = 0.04$]. To further investigate whether the inconsistent mean RT increase for probes from 2nd to 3rd position would be resolved with higher power, a pooled analysis across the three experiments was performed ($N = 55$). This revealed a marginal RT increase from 2nd to 3rd position [$t(54) = -1.55$, $p = .063$, $d = 0.15$], suggesting that this overall increase was highly variable across subjects. Finally, the RT of the control movement was significantly higher than the movement associated with the last position (4th) of the planned sequence [paired samples *t* test: $t(17) = 3.04$, $p = .007$, $d = 0.86$, two-tailed].

Across experiments, the present RT data show that during sequence planning, correct finger presses associated with earlier positions in a sequence can be selected and executed quicker than those associated with later positions, suggesting a position-dependent preactivation gradient. In particular, the latter can switch flexibly trial-by-trial, depending on which finger sequence is retrieved and planned in a particular trial. The data also suggest that the availability is modulated up to three positions ahead, with RT increases for later positions becoming less consistent across subjects. Finally, although the movement associated with the last position was the slowest to execute on average, it was still faster than a control movement not featuring in the planned sequence.

Error rates to movement probes. Figure 2.2b shows the percent press error increase relative to the error rates for the movements associated with the first position, respectively (*cf.* Supplemental Figure S2b for raw press error rates / Supplemental Figure A.S2b in Appendix A; Supplemental Table S1a for statistics / Supplemental Table A.S1a in Appendix A). *Experiment 1* revealed significant error increases from 1st to 2nd position [paired samples *t* test: $t(18) = -6.65$, $p < .001$, $d = 1.83$, one-tailed] and from 2nd to 3rd position [$t(18) = -1.93$, $p = .035$, $d = 0.27$], and no significant increase from 3rd to 4th position [$t(18) = -1.24$, $p = .116$, $d = 0.21$]. *Experiment 2* replicated the significant error increase from 1st to 2nd position [$t(17) = -5.51$, $p < .001$, $d = 1.57$] and from 2nd to 3rd position [$t(17) = -2.05$, $p = .029$, $d = 0.43$]. In contrast, the difference from 3rd to 4th position showed no significant increase, but an unexpected decrease of errors [$t(17) = 2.60$, $p = .010$, $d = 0.54$]. *Experiment 3* again replicated the significant error increases from 1st to 2nd position [$t(17) = -7.77$, $p < .001$, $d = 1.83$] and from 2nd to 3rd position [$t(17) = -1.88$, $p = .039$, $d = 0.58$], while there was no significant difference between the 3rd and 4th positions [$t(17) = 0.77$, $p = .227$, $d = 0.20$]. The control movement did not show a significant increase in errors compared with the 4th position [paired samples *t* test: $t(17) = -0.81$, $p = .430$, $d = 0.26$, two-tailed].

The error rate data from all experiments indicate that during sequence planning, movement probes associated with earlier positions in a sequence are more likely to lead to correct finger presses than those associated with later positions, which are more prone to erroneous finger presses. Like RT, error rate data point to a position-dependent preactivation gradient for movements associated with the first three positions in the sequence, but respective error increases between the first three positions appear to be more pronounced and consistent across participants, particularly for increases from 2nd to 3rd position. Further, it shows that movements associated with the last (4th) position are equally error prone as a sequence irrelevant control movement, although the former is still faster to execute when selected correctly. Taken together, our findings advocate the presence of a preparatory preactivation gradient, which renders movements associated with later sequence positions less available for correct selection and fast execution. They point to the planning of up to three constituent movements in advance within a brief preparation period and retrieval from memory. This preactivation level does not increase linearly with movement positions but falls off and becomes more variable across participants for movements associated with later positions. The variability of the gradient during planning across participants is examined below in the context of skilled performance.

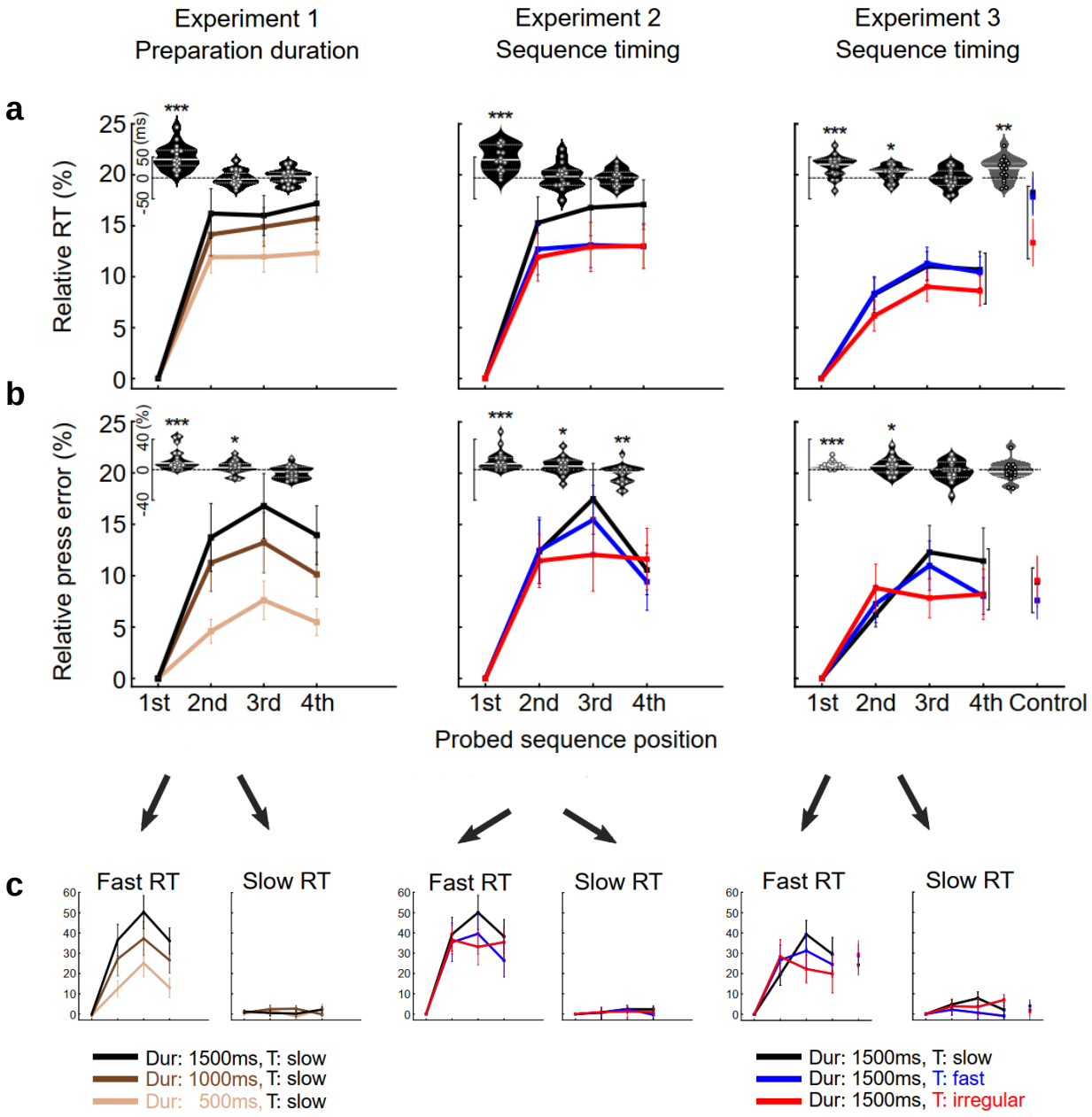


Figure 2.2 | Position-dependent movement availability during sequence planning. a. RTs for each probed sequence position relative to the first position. **b.** press errors for each probed sequence position relative to the first position. (*cf.* raw RT and press error graphs in Supplemental Figure S2, a and b or Supplemental Figure A.S2a and b in Appendix A). Both relative RT and press error were calculated from RTs and press error rates, respectively, obtained in *Probe* trials prompting the production of a movement associated with the 1st–4th press position of the planned sequence (*experiments 1, 2,* and *3*) or a control movement not present in any sequence (*experiment 3*). Black inset violin plots illustrate the position-dependent increases of raw RT and raw press error in the baseline condition (Dur: 1500 ms, T: slow), from 1st to 2nd, 2nd to 3rd, and 3rd to 4th positions. Gray inset violin plots illustrate the difference between 4th position and control across sequence conditions, as indicated by the brackets. **c.** relative press error in lower ('Fast RT') and upper ('Slow RT') RT quartiles. Error bars in line graphs represent standard errors. In inset violin plots, solid white lines represent the median, and lower and upper dashed white lines represent the 25th and 75th percentiles, respectively. Significance asterisks over the black inset violin plots indicate

one-tailed increases (position-dependent increases in RT and error rate), whereas the asterisks over the gray inset violin plots represent significance for a two-tailed test (increases or decreases in availability relative to control movement). *$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$. Dur, duration; RT, reaction time; T, timing.

2.5.2 Position-dependent differences in movement availability are modulated by preparation duration, not timing

Next, we examined whether the position-dependent availability for correct movement selection and fast execution during planning is modulated by the time to prepare a sequence, or the planned sequence timing.

Preparation duration. According to our accuracy hypothesis, a more accurate plan of the sequence progressively established across preparation durations of 500-1500 ms would lead to an expansion of the preactivation gradient (Kornysheva et al., 2019). In *experiment 1* (*cf.* Supplemental Table S1b for statistics / Supplemental Table A.S1b in Appendix A), we found a large significant interaction of Position and Preparation Duration for error rates [4 x 3 repeated measures ANOVA of raw press error rates: $F(6, 108) = 3.35$, $p = .005$, $\eta^2p = .16$). The latter was driven by a significant error rate increase for 2nd relative to 1st sequence positions with longer preparation duration [500 *vs* 1500 ms preparation duration, $F(1, 18) = 15.89$, $p = .001$, $\eta^2p = .47$]. This contrast was also significant for RTs [$F(1, 18) = 5.89$, $p = .026$, $\eta^2p = .25$], although the interaction between Position and Preparation Duration for RTs did not reach significance [4 x 3 repeated measures ANOVA of raw RTs: $F(6, 108) = 2.07$, $p = .063$, $\eta^2p = .10$]. This shows that the increase in RT and error rate from 1st to 2nd position became more pronounced with longer preparation durations, an effect which drove the significant interaction.

Importantly, both the relative RT and error differences became more pronounced with longer preparation duration conditions [one-way repeated measures ANOVA of: relative RT differences - *experiment 1*, $F(2, 36) = 4.38$, $p = .020$, $\eta^2p = .20$; relative error differences - *experiment 1*, $F(2, 36) = 3.46$, $p = .042$, $\eta^2p = .16$; *cf.* Supplemental Table S1c for statistics / Supplemental Table A.S1c in Appendix A]. Thus, more time to prepare the sequence made the probed movements associated with later positions less available for correct selection and fast execution, and vice versa. This suggests that the preactivation state of the planned movements became more differentiated according to position and the preactivation gradient expanded across the sequence retrieval and preparation period.

Timing. According to the timing hypothesis, movements in a sequence that are closer in time should have more similar levels of preactivation, and vice versa, leading to a contraction and expansion of the preactivation gradient for each action. Contrary to the timing hypothesis, the interaction between Position and Timing (*cf.* Supplemental Table S1b for statistics / Supplemental Table A.S1b in Appendix A) did not reach significance, neither for RTs, nor for error rate increases [4 x 3 repeated measures ANOVA of: raw RTs - *experiment 2*, $F(3.27, 55.54) = 2.30$, $p = .082$, $\eta^2p = .12$, Greenhouse-Geisser corrected, $\chi^2(20) = 42.61$, $p = .003$; *experiment 3*, $F(3.87, 65.79) = 0.98$, $p = .426$, $\eta^2p = .05$, Greenhouse-Geisser corrected, $\chi^2(20) = 34.06$, $p = .028$; raw error rates - *experiment 2*, $F(6, 102) = 1.86$, $p = .095$, $\eta^2p = .10$; *experiment 3*, $F(6, 102) = 1.02$, $p = .416$, $\eta^2p = .06$]. This finding was corroborated by an absent effect of timing on either the relative RT or the relative error differences [one-way repeated measures ANOVA of: relative RT differences - *experiment 2*, $F(1.48, 25.23)= 0.68$, $p = .475$, $\eta^2p = .04$, Greenhouse-Geisser corrected, $\chi^2(2) = 6.83$, $p = .033$; *experiment 3*, $F(2, 34) = 1.92$, $p = .162$, $\eta^2p = .10$; relative error differences - *experiment 2*, $F(2, 34) = 0.00$, $= 0.999$, $\eta^2p = .00$; *experiment 3*, $F(1.27, 21.52) = 1.50$, $p = .241$, $\eta^2p = .08$, Greenhouse-Geisser corrected, $\chi^2(2) = 13.87$, $p = .001$; *cf.* Supplemental Table S1c for statistics / Supplemental Table A.S1c in Appendix A]. We investigated whether the results may be contaminated by participants that considerably deviated in their relative temporal error performance (memory-guided *Sequence* trials; test phase). Therefore, we performed the same analyses after removing outlier participants that showed little modulation of timing during sequence production (*cf.* Supplemental Figure S3; see https://doi.org/10.6084/m9.figshare.13168514 or Supplemental Figure A.S3 in Appendix A). However, without these outliers, the interaction between Position and Timing was still not significant. Overall, these analyses indicate that preparing a sequence that is twice as fast, or temporally grouped, did not impact the position-dependent preactivation gradient of movements during sequence planning.

2.5.3 Position-dependent modulation of press error during planning is revealed through fast responses to probes

Next, we sought to determine whether the characteristic position-dependent increases in press errors in *Probe* trials were driven by automatic responses to *Probe* cues or by deliberate movement selection. To investigate this question, we analyzed the position-dependent error increases for the first versus last RT distribution quartiles in each participant (baseline condition:

1500 ms preparation duration and slow timing). Figure 2.2c (*cf.* Supplemental Table S1a for statistics / Supplemental Table A.S1a in Appendix A) illustrates the press error increases relative to the first position for fast and slow RT quartiles. In fast response trials, we found significant error increases up to the 3rd position in *experiments 1* and *3* [paired samples *t* tests: *experiment 1*, 1st to 2nd position, $t(18) = -6.54$, $p < .001$, $d = 0.54$, one-tailed; 2nd to 3rd position, $t(18) = -2.87$, $p = .005$, $d = 0.40$; 3rd to 4th position, $t(18) = 3.12$, $p = .003$, $d = 0.48$; *experiment 3*, 1st to 2nd position, $t(17) = -6.59$, $p < .001$, $d = 2.12$; 2nd to 3rd position, $t(17) = -1.82$, $p = .043$, $d = 0.55$; 3rd to 4th position, $t(17) = 1.63$, $p = .061$, $d = 0.35$] and up to the 2nd position in *experiment 2* [1st to 2nd position, $t(17) = -6.99$, $p < .001$, $d = 1.57$; 2nd to 3rd position, $t(17) = -0.93$, $p = .184$, $d = 0.43$; 3rd to 4th position, $t(17) = 1.43$, $p = .085$, $d = 0.54$]. In contrast, in slow response trials, errors did not increase significantly with position [*experiment 1*, 1st to 2nd position, $t(18) = 0.59$, $p = .281$, $d = 0.20$; 2nd to 3rd position, $t(18) = -0.55$, $p = .294$, $d = 0.19$; 3rd to 4th position, $t(18) = -0.60$, $p = .277$, $d = 0.16$; *experiment 2*, 1st to 2nd position, $t(17) = -0.57$, $p = .290$, $d = 0.20$; 2nd to 3rd position, $t(17) = 0.00$, $p = .500$, $d = 0.00$; 3rd to 4th position, $t(17) = 0.57$, $p = .290$, $d = 0.20$; *experiment 3*, 1st to 2nd position, $t(17) = -0.34$, $p = .368$, $d = 0.08$; 2nd to 3rd position, $t(17) = 0.15$, $p = .443$, $d = 0.04$; 3rd to 4th position, $t(17) = 0.54$, $p = .299$, $d = 0.17$]. The control movement did not show more errors than the 4th position in either fast or slow RT as in the main results [fast RTs, $t(17) = -0.95$, $p = .353$, $d = 0.28$, two-tailed; slow RTs, $t(17) = 0.10$, $p = .922$, $d = 0.03$].

These results demonstrate that the position-dependent availability of movements for correct selection following movement *Probe* cues is driven by automatic responses rather than by a cognitive selection process.

2.5.4 Incorrect presses to movement probes during planning are dominated by the movement in the first sequence position

We investigated whether incorrect presses in *Probe* trials were associated with specific positions of the planned sequence on that trial (Figure 2.3; *cf.* Supplemental Table S2 for statistics; see https://doi.org/10.6084/m9.figshare.13673668 or Supplemental Table A.S2 in Appendix A). This was undertaken for each probed position separately and across all three experiments. Results for 1st position (Figure 2.3, upper left) did not yield significant differences among the press rate for 2nd, 3rd, and 4th positions [one-way repeated measures ANOVA: $F(2, 108) = 0.63$, $p = .535$, $\eta^2 p = .01$]. In contrast, probing the movements associated with 2nd, 3rd, and 4th positions revealed

that participants consistently selected the 1st position more frequently. Specifically, when the 2nd position was probed (Figure 2.3, upper right), there was a significant difference among 1st, 3rd, and 4th erroneously pressed positions [$F(1.38, 74.36) = 84.70$, $p < .001$, $\eta^2 p = .61$, Greenhouse-Geisser corrected, $\chi^2(2) = 31.92$, $p < .001$; 1st position higher than 3rd position, $p < .001$; 1st position higher than 4th position, $p < .001$; 3rd position higher than 4th position, $p = .007$]. Similarly, the press rate for the 1st position when the 3rd position was probed (Figure 2.3, lower left) was higher than the 2nd and 4th pressed positions [$F(1.34, 72.50) = 84.90$, $p < .001$, $\eta^2 p = 0.61$, Greenhouse - Geisser corrected, $\chi^2(2) = 35.65$, $p < .001$; 1st position higher than 2nd position, $p < .001$; 1st position higher than 4th position, $p < .001$; 2nd position marginally lower than 4th position, $p = .069$]. The 4th probed position (Figure 2.3, lower right) produced higher 1st position presses [$F(1.54, 83.34) = 42.95$, $p < .001$, $\eta^2 p = 0.44$, Greenhouse-Geisser corrected, $\chi^2(2) = 18.60$, $p < .001$; 1st position higher than 2nd position, $p < .001$; 1st position higher than 3rd position, $p < .001$; 2nd position not significantly higher than 3rd position, $p = 1.000$].

The distribution of erroneous presses shows that the movement availability was highly biased toward the production of the movement in the first position in each respective sequence upon retrieval and planning of the cued sequence.

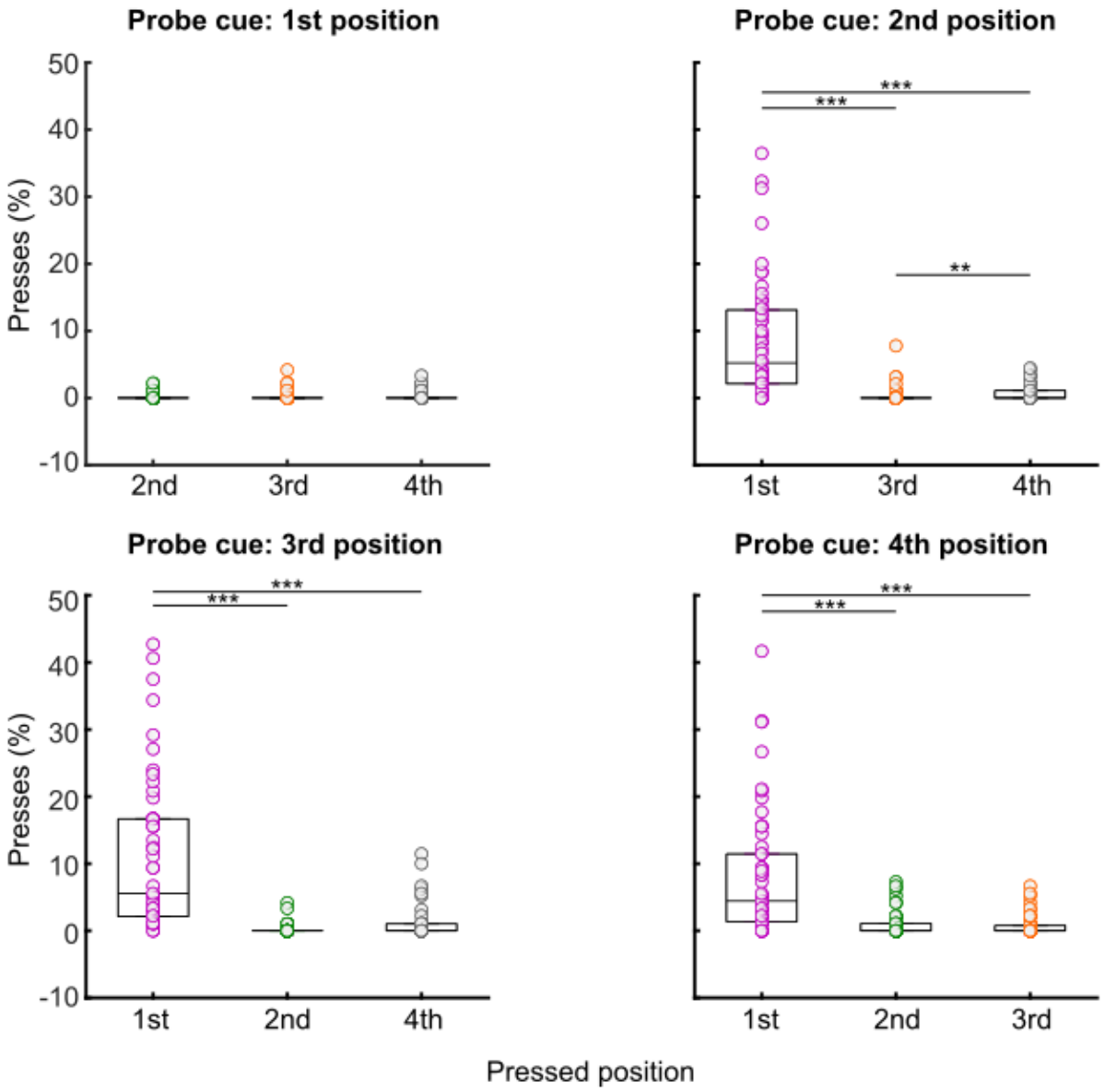


Figure 2.3 | Pattern of press errors for probed movements associated with different sequence positions. Incorrect presses per probed position across experiments are shown in percent of all responses. $^{**}p \leq 0.01$, $^{***}p \leq 0.001$.

2.5.5 Greater position-dependent differences in movement availability during planning predict better performance

Position-dependent preactivation differences between sequential movement patterns during planning have been shown to predict the participants' subsequent performance accuracy (Kornysheva et al., 2019). Specifically, the distance (i.e., difference) between the neural pattern probabilities of consecutive movements during planning predicted more skilled sequence execution. Accordingly, we predicted that larger position-dependent differences in availability of movements for correct selection and fast execution during planning would correlate with a more skilled performance during sequence execution. Position-dependent differences in availability of movements was considered a proxy measure for the preactivation gradient size (*cf.* relative RT and error differences in Data Analysis, Materials and Methods). We took faster initiation of correct sequences after the *Go* cue, as well as reduced relative temporal errors and finger errors as markers of a more skilled performance. Correlation analyses were performed on group data (N = 55) obtained from trials in the baseline condition present in all experiments [long preparation duration and slow timing conditions; Figure 2.4, a and b; *cf.* Supplemental Figure S4 for raw RT and error differences (see https://doi.org/10.6084/m9.figshare.13168628 or Supplemental Figure A.S4 in Appendix A); Supplemental Table S3a for statistics (see https://doi.org/10.6084/m9.figshare.13673734 or Supplemental Table A.S3a in Appendix A)]. Results showed that participants with larger relative RT and error differences during planning initiated correct sequences faster (relative RT differences: r = -.39, p = .002; relative error differences: r = -.54, p < .001, one-tailed). Larger relative RT differences during planning were also correlated with lower relative temporal error (r = -.35, p = .005). This association did not hold up for the relative error differences (r = -.05, p = .356). Thus, the latter may be a less sensitive predictor for temporal accuracy than the relative RT differences. In contrast to our predictions, we did not find an association with finger error (relative RT differences: r = .08, p = .273; relative error differences: r = .12, p = .196). This was likely due to ceiling effects in finger press accuracy performance attributable to the limited number of trained finger sequences.

To inspect the position-dependent slopes in movement availability based on sequence performance, we performed median split-based initiation RT, relative temporal error, and finger error (Figure 2.4 insets; *cf.* Supplemental Table S3b for statistics / Supplemental Table A.S3b in Ap-

pendix A). Participants with faster initiation RTs exhibited larger position-dependent RT differences (Figure 2.4a, inset) compared with those with slower initiation RTs [mixed ANOVA with median split of initiation RT: main effect of Group, $F(1, 53) = 33.63$, $p < .001$, $\eta^2p = .39$; Position x Group, $F(3, 159) = 5.70$, $p = .001$, $\eta^2p = .10$]. Equally, the position-dependent press error differences (Figure 2.4b, inset) were steeper for participants with fast initiation RTs [mixed ANOVA with median split of initiation RT: main effect of Group, $F(1, 53) = 10.77$, $p = .002$, $\eta^2p = .17$; Position x Group, $F(3, 159) = 3.90$, $p = .010$, $\eta^2p = .07$]. Median splits by relative temporal error or finger error did not show differences in movement availability during planning, confirming further that this relationship is either more subtle (temporal error) or absent (finger error).

Together, these analyses show that behavioral markers of a more expanded preactivation gradient can predict faster initiation of correct finger sequences and improved relative temporal, but not finger accuracy during production.

Next, we conducted a series of extended analyses focusing on sequence production. These additional analyses examined whether participants - on average - produced the sequences from memory with accurate relative timing, and whether preparation time and sequence timing conditions changed performance, i.e., speed of correct sequence initiation, as well as temporal and finger accuracy.

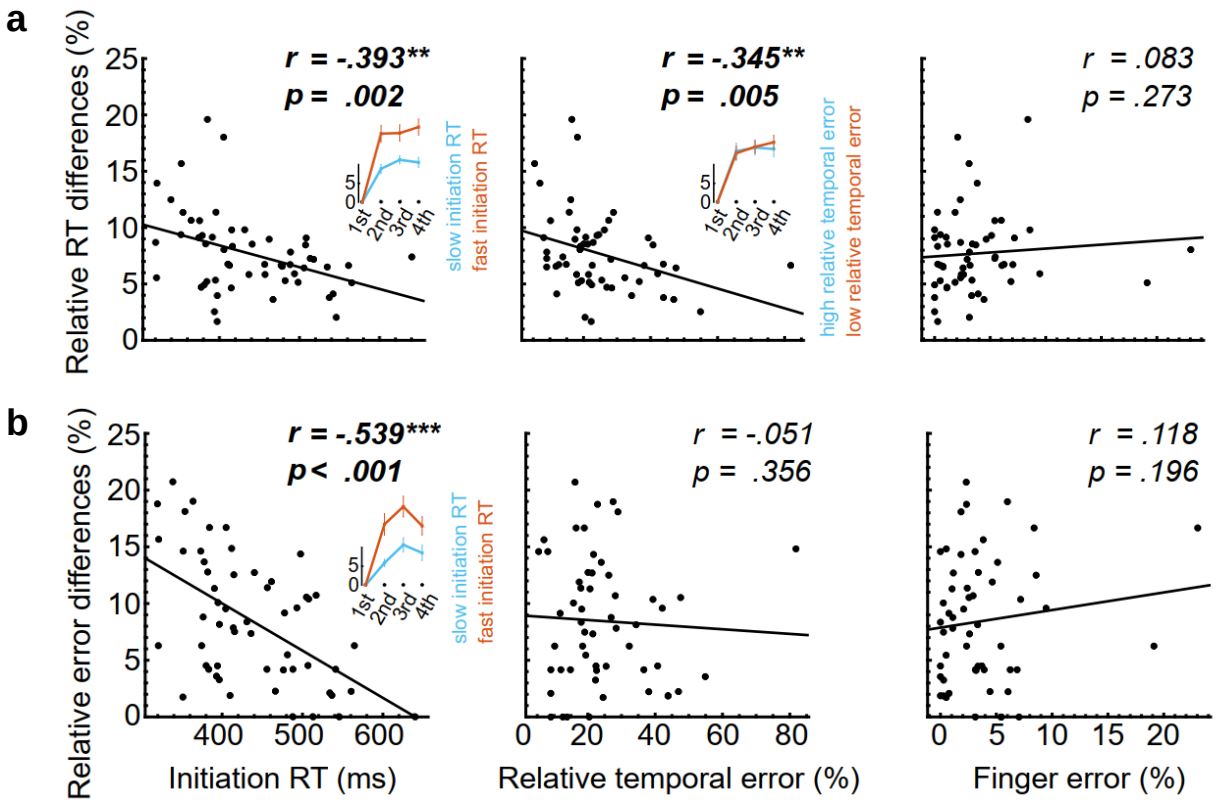


Figure 2.4 | Correlation of performance with position-dependent differences in movement availability during planning. The mean difference between adjacent positions (1st–2nd, 2nd–3rd, 3rd–4th) based on RTs and press errors relative to the first position (*Probe* trials) was taken as a proxy for the preactivation gradient size during preparation, with steeper (larger) differences reflecting a more expanded gradient (*cf.* raw RT and error differences in Supplemental Figure S4 or Supplemental Figure A.S4 in Appendix A). **a.** Correlations between relative position-dependent differences in RT in *Probe* trials and each of the performance measures (initiation RT, relative temporal error, and finger error). **b.** Correlations between relative position-dependent differences in error rate in *Probe* trials and each of the performance measures (initiation RT, relative temporal error, and finger error). Inset graphs in each panel illustrate relative position-dependent RT (**a**) and press error (**b**) increases during planning for participants with faster *vs* slower initiation RT and lower *vs* higher relative temporal error performance (median splits). Error bars represent standard errors. All correlations are one-tailed, in line with one-sided predictions regarding the beneficial effect of a differentiated preactivation of sequence movements during planning. RT, reaction time. $^{**}p \leq 0.01$, $^{***}p \leq 0.001$.

2.5.6 Participants produced sequences from memory with correct relative timing

Participants were trained to either retain the same (*experiment 1*) or consistently modulate (*experiments 2* and *3*) the relative timing during sequence production across sequence conditions. On average, participants produced the sequences with timing relative to the target IPIs [Figure 2.5a; *cf.* Supplemental Table S4 for statistics (see https://doi.org/10.6084/m9.figshare.13673800

or Supplemental Table A.S4 in Appendix A); Supplemental Figure S5 for mean absolute press timing per trial (see https://doi.org/10.6084/m9.figshare.13168649 or Supplemental Figure A.S5 in Appendix A)].

The mean relative timing of finger presses in *experiment 1* was nearly identical across preparation duration conditions (Figure 2.5a, left). Nevertheless, we detected a small but significant interaction between IPI and Preparation Duration [3 × 3 repeated measures ANOVA: $F(4, 72) = 2.53$, $p = .048$, $\eta^2 p = .12$], explained by IPI modulations of 9 ms across conditions. Post hoc comparisons (Bonferroni-corrected for nine tests) revealed a significant shortening of the 1st interval in the short preparation duration ($p = .002$) and of the 1st ($p = .002$) and 3rd ($p = .004$) intervals in the intermediate compared with the long preparation duration. This shows that there was a tendency to slightly compress the 1st and 3rd intervals with shorter preparation time. If there were a timing confound on sequence planning duration in *experiment 1*, the timing effect should have been vastly amplified by the experimental modulation of timing requiring the doubling or halving of IPIs in *experiments 2* and *3*. However, we did not observe any strong and consistent effect of the latter on sequence planning.

Experiment 2 (Figure 2.5a, middle) showed a large significant interaction of IPI and Timing [3 x 3 repeated measures ANOVA: $F(1.26, 21.42) = 59.49$, $p < .001$, $\eta^2 p = .78$, Greenhouse-Geisser corrected, $\chi^2(9) = 97.83$, $p < .001$], in line with the task instructions. The pairwise comparisons (Bonferroni-corrected for nine tests) of the produced IPIs confirmed that the participants modulated their relative timing according to the target IPI structure. In accordance with the cued sequence, the 1st IPI was significantly longer in the slow than in the fast ($p < .001$) and the irregular timing conditions ($p < .001$), while it did not differ in the fast versus irregular timing conditions ($p = 1.000$). The 2nd IPI length increased slightly, yet proportionally for both the slow and fast timing conditions, retaining the significant difference ($p < .001$) and doubled in length in the irregular relative to the slow timing condition ($p < .001$). The 3rd IPI exhibited a very similar profile to the 1st IPI (slow *vs* fast, $p < .001$; slow *vs* irregular, $p < .001$), but its length decreased slightly in the fast compared with the irregular timing condition ($p = .027$). *Experiment 3* (Figure 2.5a, right) replicated the findings of *experiment 2* showing a significant interaction of IPI and Timing [3 x 3 repeated measures ANOVA: $F(1.56, 26.49) = 17.37$, $p < .001$, $\eta^2 p = .51$, Greenhouse-Geisser corrected, $\chi^2(9) = 61.31$, $p < .001$]. Again, post hoc pairwise comparisons (Bonferroni-corrected for nine tests) confirmed that the 1st IPI in the slow timing was longer than that in the fast ($p = .001$)

and irregular (p = .003) timing conditions, while no difference was found between the fast and irregular timing conditions (p = 1.000). The 2nd IPI was significantly longer in the slow compared with the fast timing condition (p = .001), but shorter compared with the irregular timing condition (p = .005). Similarly, the 2nd IPI in the fast timing was half as long than in the irregular timing condition (p < .001). The 3rd IPI was twice as long in the slow compared with the fast timing condition (p < .001). It did not show a significant shortening for the irregular timing when compared with the slow timing condition (p = 1.000) and showed only a marginally significant difference between the fast and irregular timing conditions (p = .096).

Overall, these results demonstrate that, on average, participants produced the finger sequences from memory with accurate relative timing across conditions.

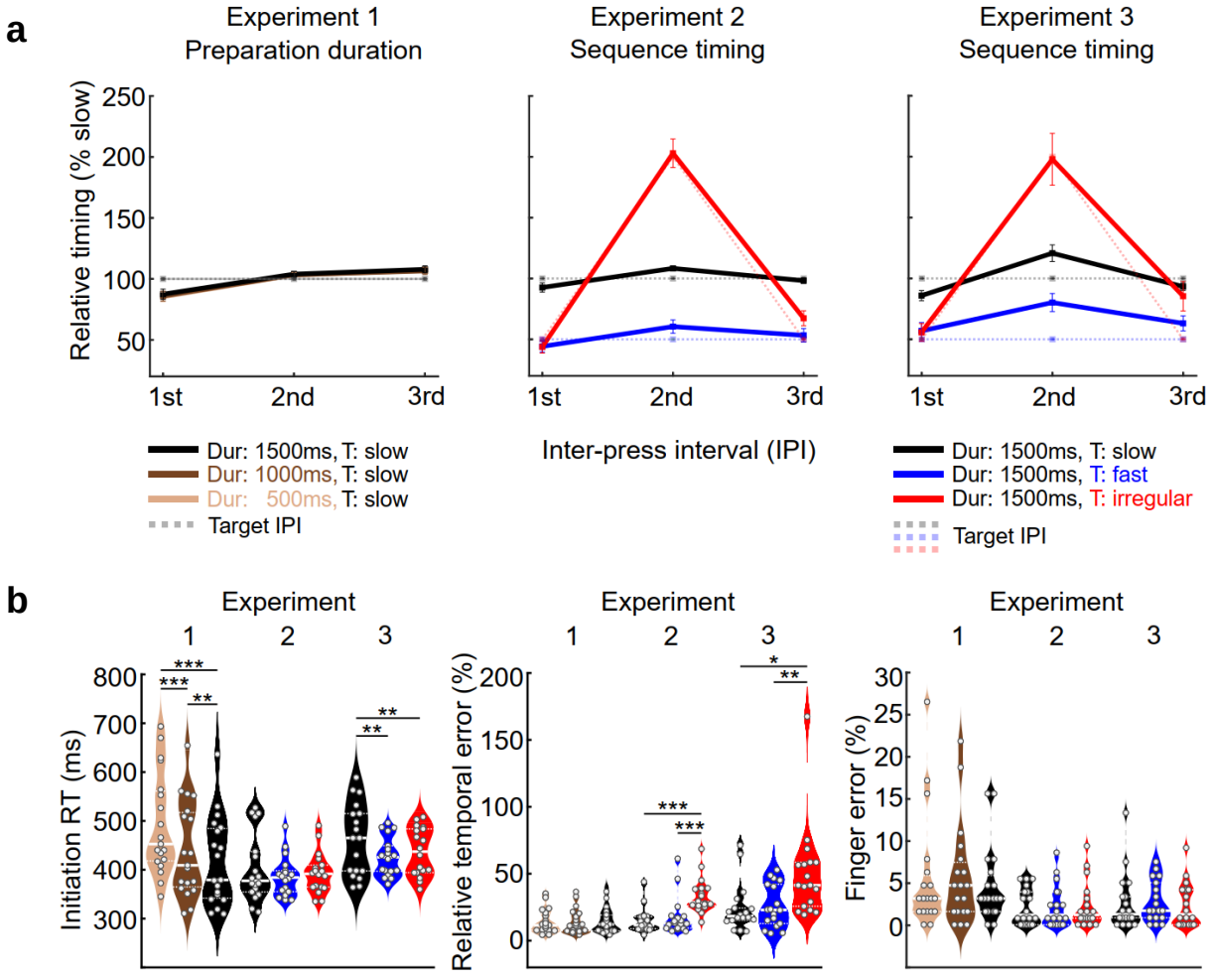


Figure 2.5 | Sequence production. a. Relative timing as a function of IPI production of a slow, twice as fast, and an irregular sequence. Both the produced (solid lines) and target IPIs (dashed lines) were normalized across trials

relative to the baseline condition (Dur: 1500 ms, T: slow). Error bars represent standard errors. **b.** Sequence initiation RT (*Go* cue to first press latency), relative temporal error, and finger error (proportion of trials with incorrect presses) in each experimental condition (preparation duration, *experiment 1*; timing, *experiments 2* and *3*). Solid white lines represent the median, and lower and upper dashed white lines represent the 25th and 75th percentiles, respectively. *$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$. Dur, duration; RT, reaction time; T, timing; IPI, inter-press interval.

2.5.7 Longer preparation durations shortened initiation of correct sequences

We found a significant difference in sequence initiation RT with Preparation Duration [one-way repeated measures ANOVA: *experiment 1*, $F(1.38, 24.88) = 52.81$, $p < 0.001$, $\eta^2p = .75$, Greenhouse-Geisser corrected, $\chi^2(2) = 10.07$, $p = .006$; Figure 2.5b, left; *cf.* Supplemental Table S4 for statistics / Supplemental Table A.S4 in Appendix A]. Pairwise comparisons (Bonferroni-corrected for three tests) confirmed that sequence initiation RT was significantly faster for the intermediate (1000 ms) and long (1500 ms) preparation duration than following a short (500 ms) preparation duration (intermediate *vs* short, $p < .001$; long *vs* short, $p < .001$). Further, sequence initiation RT following a long preparation duration was significantly faster as compared with the intermediate preparation duration ($p = .005$). In experiments with single movements, the effect of variable preparation duration on RT is known as the foreperiod effect (Foley, 1959; Vallesi et al., 2007). It can be accounted for by generic motor preparedness due to heightened temporal expectation (hazard rate) for longer preparation durations (Bueti et al., 2010) and includes carry-over effects across trials (Langner et al., 2018; Steinborn & Langner, 2012) (*cf.* Supplemental Figure S6 for preparation duration effects of preceding trials in *experiment 1*; see https://doi.org/10.6084/m9.figshare.13675330 or Supplemental Figure A.S6 in Appendix A). However, the effect on initiation RT reported here cannot be attributed to *general* temporal preparedness alone. In contrast to classical foreperiod paradigms, the current paradigm involves a *Sequence* cue at the start of the foreperiod, instead of a neutral warning signal. Therefore, a facilitation of initiation RT will reflect the state of sequence preparedness that increases with longer durations (Ariani & Diedrichsen, 2019; Sternberg et al., 1978), not just nonspecific effects of temporal expectation.

There was no main effect of Timing on sequence initiation RT in *experiment 2* [one-way repeated measures ANOVA: $F(1.41, 23.92) = 1.70$, $p = .207$, $\eta^2p = .09$, Greenhouse-Geisser corrected, $\chi^2(2) = 8.76$, $p = .013$], but a main effect of Timing in *experiment 3* [one-way repeated measures ANOVA: $F(1.29, 21.99) = 11.59$, $p = .001$, $\eta^2p = .41$, Greenhouse-Geisser corrected,

$\chi^2(2) = 12.63$, $p = .002$]. As explained by pairwise comparisons (Bonferroni-corrected for three tests), participants in *experiment 3* were slower at initiating a sequence of slow timing when compared with fast timing ($p = .006$) and irregular timing ($p = .010$). There was no difference in initiation RT between the fast and the irregular timing conditions ($p = .118$). This effect was not consistent across *experiments 2* and *3*, but present at the mean level in both experiments. This implies that sequences with a slow isochronous timing structure were less prepared for initiation following a *Go* cue compared with sequences that started with two presses in short succession (fast and irregular timing structures), which may be more prone to a rushed initiation.

2.5.8 Sequences involving irregular inter-press intervals were produced with less accurate timing

Next, we established whether preparation duration (*experiment 1*) and sequence timing (*experiments 2* and *3*) modulated relative temporal error during sequence production (Figure 2.5b, middle; *cf.* Supplemental Table S4 for statistics / Supplemental Table A.S4 in Appendix A). In *experiment 1*, mean relative temporal error did not differ among the three preparation duration conditions [one-way repeated measures ANOVA: $F(2, 36) = 0.11$, $p = .901$, $\eta^2p = .01$]. Here, relative temporal performance may have been compensated in the short preparation duration condition by slower initiation RT (*cf.* above). In *experiment 2*, there was a significant effect of Timing [one-way repeated measures ANOVA: $F(2, 34) = 28.23$, $p < .001$, $\eta^2p = .62$]. Pairwise comparisons (Bonferroni-corrected for three tests) revealed that participants performed at a lower relative temporal error when producing a sequence of slow timing compared with irregular timing ($p < .001$) and a sequence of fast timing compared with irregular timing ($p < .001$), whereas there was no difference between sequences in the slow versus fast timing conditions ($p = 1.000$). *Experiment 3* replicated the main effect of Timing [one-way repeated measures ANOVA: $F(1.45, 24.72) = 7.06$, $p = .007$, $\eta^2p = .29$, Greenhouse-Geisser corrected, $\chi^2(2) = 7.53$, $p = .023$]. In line with the findings of *experiment 2*, there were less relative temporal errors in the slow timing ($p = .049$) and fast timing ($p = .008$) conditions when compared with the irregular timing condition. Again, there was no significant difference in relative temporal performance between the two isochronous conditions (slow *vs* fast, $p = 1.000$). In sum, the production of sequences which consisted of non-isochronous IPIs (irregular timing condition) as opposed to equal IPI lengths (isochronous timing conditions; slow, fast) were associated with decreased relative temporal accuracy.

2.5.9 Finger press accuracy in sequences produced from memory was matched across conditions

In the test phase, participants produced finger press sequences entirely from memory. Neither Preparation Duration [one-way repeated measures ANOVA: *experiment 1*, $F(2, 36) = 0.23$, $p = .795$, $\eta^2p = .01$] nor Timing [one-way repeated measures ANOVA: *experiment 2*, $F(2, 34) = 0.02$, $p = .984$, $\eta^2p = .00$; *experiment 3*, $F(2, 34) = 0.96$, $p = .394$, $\eta^2p = .05$] affected finger error during sequence production (Figure 2.5b, right; *cf.* Supplemental Table S4 for statistics / Supplemental Table A.S4 in Appendix A). This means that participants prepared the finger order of cued sequences with the same accuracy, regardless of the preparation time or temporal structure of the planned sequence. Note that finger error in sequence production was higher in *experiment 1* than in *experiments 2* and *3*. This is likely due to *experiment 1* involving sequences of two different finger sequences on a trial-by-trial basis, whereas *experiments 2* and *3* involved the same finger sequence performed with different timing.

2.6 Discussion

Sequence planning is central to skilled action control; however, its content and structure is poorly understood (Bullock, 2004a; Remington, Egger, et al., 2018). Neurophysiological findings have demonstrated that a trained movement sequence is preplanned by establishing a competitive preactivation gradient of movement patterns according to their serial position, and that the quality of this neural pattern during planning predicts subsequent performance (Averbeck et al., 2002; Basu & Murthy, 2020; Kornysheva et al., 2019; Pinet et al., 2019). Here, we report a putative behavioral marker of this competitive preactivation gradient. During a short retrieval and preparation period, we measured the behavioral availability of each constituent movement of the planned sequence for accurate and fast production. Our findings show that behavioral availability is dependent on the sequence position the respective movements are associated with, mirroring the preactivation gradient observed in neurophysiological studies (Averbeck et al., 2002; Kornysheva et al., 2019) as predicted by CQ models (Bullock, 2004a; Hartley et al., 2016; Hartley & Houghton, 1996; Houghton, 1990). Critically, a stronger differentiation between the state of movements assigned to consecutive sequence positions correlated with markers of skilled production - the speed

of correct sequence initiation and the temporal production accuracy. In contrast, the latter did not reliably reflect the sequence production speed, or the IPI pattern of the planned sequence.

Sequence planning markedly contrasts with mechanisms for nonsequential movement planning involving multiple movement options: In the latter, a cued set of possible movements triggers equal activity increase in cortical populations tuned to the respective movements, and the preparatory competition is only resolved once a cue specifies the target movement (Cisek & Kalaska, 2005). In contrast, sequence planning established a fine-tuned gradient of movement pre-activations, with the latter switching flexibly on a trial-by-trial basis, in line with the retrieved sequence. Notably, movements that were part of the planned sequence were executed faster than a control movement, which was not part of the retrieved sequence (Figure 2.2a, right). This suggests that all constituent movements were concurrently preactivated above a passive baseline, albeit to a different degree depending on their position in the planned sequence.

Our study provides a measure of the competitive state of constituent movements before sequence production. This is complementary to previous behavioral work that supports the presence of CQ of sequence presses *during* production, such as accuracy and RT curves obtained from sequence execution (B. J. Rhodes et al., 2004; Verwey & Abrahamse, 2012), or on-the-fly movement planning following sequence initiation, assessed behaviorally (Behmer & Crump, 2017) and through measures of cortico-spinal excitability (Behmer et al., 2018). Gilbert and colleagues have employed a paradigm at the interface between sequence preparation and production to characterize the CQ profile of the respective sequential movements - silent rehearsal (Gilbert et al., 2017). Here, participants were asked to listen to sequences of spoken digits and silently rehearse the items during a retention interval. They received explicit instructions to rehearse the sequence at the same pace as active production. After an unpredictable delay, a tone prompted the report of an item being rehearsed at that moment and revealed graded overlapping probabilities of neighbouring items, suggesting potential CQ during internal rehearsal. In contrast to the latter study, our paradigm did not enable active rehearsal during preparation: First, our participants retrieved the sequence entirely from memory without a sensory instruction period which might have facilitated active entrainment with the sequence before planning. Second, the period for sequence retrieval and planning was comparatively brief (ranging from 500 to 1500 ms after *Sequence* cue onset) and not sufficient to cycle through the full sequence at the rate participants employed for active production. In addition, if the observed CQ gradient were somehow driven by silent rehearsal at the

target rate, it would have been more pronounced for the fast sequences, as more of the planned sequence could fit into the preparation phase. However, there was no significant difference between relative availability of probed movements for fast and slow sequences.

Whilst active motor rehearsal at scale during the short preparation phase is unlikely, an alternative *serial* preparation mechanism may be related to rapid sequence replay. The latter has been observed in the hippocampus during navigation tasks (Ólafsdóttir et al., 2018) and perceptual sequence encoding (Liu et al., 2019), as well as in the motor cortex in the context of motor sequence learning tasks (Eichenlaub et al., 2020). Replay has been shown to involve fast sweeps through the neural patterns associated with the sequence during wakeful rest and planning (preplay) (Drieu & Zugaro, 2019; Eichenlaub et al., 2020; Jafarpour et al., 2014; Ólafsdóttir et al., 2018) and is characterized by a multifold temporal compression (Eichenlaub et al., 2020; Kurth-Nelson et al., 2016; Liu et al., 2019; Michelmann et al., 2019). How replay could translate into a parallel preactivation of serial movements reported here is uncertain. One possibility is that serial sweeps during motor sequence planning involve fast repeated replay fragments (Davidson et al., 2009; Michelmann et al., 2019) of different length during preparation, starting with the first elements - e.g., 1st-2nd-3rd, 1st-2nd, 1st, 1st-2nd-3rd-4th, 1st-2nd etc. This would produce an overall bias toward the preactivation of earlier rather than later parts of the planned sequence. This, in turn, may be translated into a cumulative ramping activity for each constituent movement by a separate downstream neuronal mechanism during the preparation period (Cisek & Kalaska, 2005; N. Li et al., 2016). Analysis of the 'sequenceness' of the corresponding neural patterns (Eichenlaub et al., 2020; Liu et al., 2019) during preparation should shed light on the presence of preplay and its possible relationship to the competitive preactivation of movements during planning (Kornysheva et al., 2019).

Characteristic differences in press error rate to movement probes were revealed through faster rather than slower responses after the *Probe* cue (Figure 2.2c). This suggests that the competitive preactivation gradient established during the short phase of sequence retrieval and planning is driven by a rapid automatic process and is not a result of slow deliberation or higher-level decision making. Contrary to a prominent account of sequence learning (Krakauer & Mazzoni, 2011; Wong & Krakauer, 2019), we suggest that the reported behavioral differences in sequence press availability reflect mechanisms of rapid and automatic planning for the production of discrete motor sequences from memory.

Remarkably, longer preparation reinforced the competitive preactivation making responses to movement probes associated with later sequence positions even slower and more inaccurate relative to those associated with earlier positions. This is counterintuitive in the context of single movement performance gains from longer foreperiod durations (Niemi & Näätänen, 1981). Here, a pure foreperiod effect would dictate general benefits for RT and error rate with longer preparation durations (Steinborn et al., 2008). In contrast, we found relative benefits and costs of the latter to be position dependent. The reported differences in movement availability became more striking the longer time participants had to prepare, e.g., the error rate for probed movements associated with later positions increased further with longer foreperiods—these movements became even harder to retrieve. The preactivation gradient expansion with longer preparation suggests a dynamic refinement of the plan for sequence production during retrieval and planning. We propose that the primacy gradient (Grossberg, 1978b, 1978a) in the parallel planning layer of CQ models expands dynamically during each sequence preparation phase enhancing the organization of sequential movements with preparation time.

Furthermore, participants exhibiting more pronounced differences in availability of movements associated with neighbouring sequence positions during planning exhibited both faster initiation times and a more accurate temporal execution of the sequence after the *Go* cue, particularly when looking at position-dependent differences in RT. These findings strengthen the interpretation that an ordered competitive preactivation of movements during planning pre-empts subsequent fluency and temporal accuracy of the sequence (Kornysheva et al., 2019). The individual differences in planning are likely driven by differences in sequence learning, which are associated with an expansion of the 'planning horizon' with practice (Ariani & Diedrichsen, 2019).

Yet, we did not replicate the association of the planning gradient with finger error probability found in the latter study. This may be due to a smaller pool of timing and finger order sequences that the participants had to learn relative to the previous paradigm, and the presence of only one finger order (paired with different sequence timings) in *experiments 2* and *3*. This facilitated finger accuracy to reach ceiling levels in a substantial number of participants. Future experiments should resolve an association with finger accuracy through the inclusion of a larger pool of trained sequences to provoke more frequent finger errors. Alternatively, reaching, drawing or force production tasks would allow to quantify more fine-grained deviations from target at overall high ordinal accuracy levels of sequence production.

In contrast to preparation duration, doubling the speed of sequence production did not change the relative behavioral availability of sequential movements during planning. This suggests invariance of the preactivation gradient across sequences produced at different time scales. This transfer across speed profiles is in line with the presence of flexible motor timing and temporal scaling in dynamic neuronal populations (Goudar & Buonomano, 2018; Wang et al., 2018). Here, the assumption is that a separate neural process controls the speed of a sequence during execution, e.g., through the strength of an external input to the network involved in the generation of timed behavior (Wang et al., 2018). We found that preparing a sequence of the same length with an irregular compared with an isochronous interval structure was associated with a slight tendency for a dampened CQ gradient during sequence planning. However, this nonsignificant trend is unlikely to be the effect of temporal grouping, as the irregular interval sequence was characterized by a significant increase in temporal interval production error (Figure 2.5b, middle), associated with timing complexity—the sequencing of two different (non-isochronous) constituent temporal intervals rather than just one (isochronous). Instead, we hypothesize that longer preparation time (above 1500 ms) would have benefitted the participants and enhanced the relative preactivation gradient, in line with *experiment 1*, facilitating the formation of a more accurate plan for this more temporally complex sequence.

Our empirical data on the preordering of sequential movements do not support the integration of movement order with movement timing before sequence execution. The weighting of the availability of each movement appears to be entirely driven by its position in the planned sequence and correlated with the fluency of correct sequence initiation. Given that participants could on average correctly modulate the relative timing of the sequences, a separate preparation process for the speed and timing of the respective sequence must be assumed. The latter may take place concurrently or at different time points during preparation (Bortoletto et al., 2011; Bortoletto & Cunnington, 2010; Maslovat et al., 2018). In previous work, we proposed a drift-diffusion based model which contains input from separate modules that activate movement order and timing (Kornysheva et al., 2013). This model was based on behavioral sequence learning data demonstrating that sequence timing is encoded independently of the movement order but requires multiplicative, rather than additive integration with each movement. This enables trained sequence tim-

ing to be transferred to new sequences but only after the movement order has been acquired, reconciling previous experimental findings (Kornysheva & Diedrichsen, 2014; O'Reilly et al., 2008; Shin & Ivry, 2003; Ullén & Bengtsson, 2003; Zeid & Bullock, 2019).

Recently, Zeid and Bullock (2019) proposed how such plans may be generated in the context of CQ models. The authors propose that two separate CQ modules could operate in parallel - one controlling the item order and the other controlling the sequence of IPIS that define a rhythmic pattern, including separate parallel planning and competitive choice layers. Although this model is in line with neurophysiological and imaging evidence for a separate control of timing for sequence generation (Bengtsson et al., 2004, 2005; Crowe et al., 2014; Friston & Buzsáki, 2016; Kornysheva & Diedrichsen, 2014; Merchant, Pérez, et al., 2013), empirical support for timing being implemented via a CQ process for temporal intervals is still lacking. Behavioral paradigms are unlikely to be valuable in this context, as it is impossible to probe the planning of IPI sequences decoupled from the effector. However, neurophysiological recordings in monkeys and humans may shed further light on the organization of interval patterns before production: If temporal intervals in a sequence are competitively queued, we should expect neuronal populations preferentially tuned to temporal intervals of different durations, e.g., as found in the medial premotor cortex (Crowe et al., 2014; Merchant, Pérez, et al., 2013), to be preactivated in parallel during planning according to their respective position in the sequence, and transfer across effectors.

Alternatively, timing of discrete movements in a sequence may be controlled during execution only through the acquired cyclical dynamics of neuronal population activity. Specifically, isochronous sequences involving the same movement have been associated with circular population trajectories where each interval cycle is shifted forward along a sequence position or 'tapping manifold' resulting in a helical population trajectory (Balasubramaniam et al., 2021; Russo et al., 2020). Here, the interval duration has been linked to the amplitude size of the trajectory loops thus controlling the speed of isochronous tapping sequences. The sequence position or 'tapping manifold' may be the readout of a CQ process and thus serve as a potential interface between position, interval, and movement identity. However, it remains unclear whether such a cyclical procession of population activity is also utilized for the production of sequences with non-isochronous intervals and sequences involving multiple movements.

Conclusions

In sum, our findings indicate that the behavioral availability of movements during a brief period of retrieval and planning reflects the subsequent movement order, such that movements associated with later positions are less available for fast and accurate execution. Crucially, the competitive state of the movements appears to be invariant to the exact timing of the sequence. Instead, it is dynamically established during sequence planning and predicts the individual's subsequent sequence production fluency and accuracy. The current behavioral paradigm could provide a straightforward and cost-effective way to assess the organization of movements during sequence planning across trials in individual participants, in addition to neurophysiological approaches requiring access to neuroimaging, electrophysiology and computational resources for advanced neural pattern analysis (Averbeck et al., 2002; Kornysheva et al., 2019). This behavioral readout of the state of movements before execution may serve to advance our understanding of the neural processes associated with disorders affecting the fluent production of motor sequences, such as stuttering, dyspraxia, and task-dependent dystonia (Craig-McQuaide et al., 2014; Howell, 2007; Ingham et al., 2018; N. Miller, 1988; Sadnicka et al., 2018).

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2.9 Disclosures

No conflicts of interest, financial or otherwise, are declared by the authors.

2.10 Author Contributions

M.M. and K.K. conceived and designed research; M.M. and T.I. performed experiments; M.M., T.I., and K.K. analyzed data; M.M., T.I., G.H., and K.K. interpreted results of experiments; M.M. and K.K. prepared figures; M.M., T.I., G.H., and K.K. drafted manuscript; M.M., G.H., and K.K. edited and revised manuscript; M.M., G.H., and K.K. approved final version of manuscript.

Chapter 3

Serial order and speed modulation during motor sequence planning: Insights from EEG pattern decoding - Experiment 4

This Chapter comprises a paper in preparation. This work has been disseminated in a poster presentation at the Neural Control of Movement 2021 Conference.

Mantziara, M., Holland, P., Egan, C., Galea, J., & Kornysheva, K. (in preparation). Neural planning of sequences produced with different speeds.

3.1 Abstract

Motor sequence planning encodes information about the organization of serial order of movements and the timing of the planned sequence. Parallel preactivation of movements, graded by their serial position, form a behavioral CQ gradient that has been reported to be unaffected by planned sequence timing. We set out to address whether, at the neural level, sequence planning is organized in parallel preactivations of upcoming movements ordered by their position and modulated by sequence speed. Healthy participants were trained for two days to retrieve and produce from memory a four-finger sequence with two different timings (slow *vs* fast) and a sequence-irrelevant control effector, as prompted by abstract visual cues. We approached our question by re-testing for the behavioral CQ gradient (day 3), followed by non-invasive EEG and concurrent EMG recordings (day 4). Our behavioral results replicate the presence of a CQ preactivation gradient representing serial order of upcoming movements while being invariant of sequence speed. In contrast, EEG pattern decoding of sequential movements showed no evidence of CQ parallel preactivation. Normalization and timing analysis revealed that sequential movement-related patterns were temporally scaled during preparation and production periods to match the timing of the planned, slow or fast, sequence speed. Temporal modulation was not observed at the EMG level during preparation. The decoded control effector temporally coincided with the movement-related pattern associated with first sequence position during preparation and production at the EEG but not at the EMG level. Exploratory source reconstruction showed that the same temporal patterns were shared among subcortical, frontal, and sensorimotor areas. These findings support the presence of a high-level preparatory timing rehearsal mechanism which flexibly adjusts to the intended speed and is represented outside the CQ mechanism. Our results indicate that order and timing may be controlled by separate systems.

3.2 New & Noteworthy

Order and timing are important properties of motor sequence organization. We used behavioral movement probes and movement decoding from non-invasive EEG during sequence planning. Order was represented via a behavioral CQ preparatory mechanism. EEG decoding detected a timing rehearsal signal which flexibly transferred across planned sequences of different speeds. Order and timing may be represented independently suggesting modular control of spatiotemporal movement sequences.

Keywords: *EEG decoding; EMG decoding; Competitive queuing; Serial order; Temporal scaling; Motor sequence planning*

3.3 Introduction

We interact with the world through complex motor behaviors that encompass the planning and execution of sequential movements. Intrinsic to skilled sequencing is the ability to control movements in a predefined order and, often, adaptable timing, such as at different speeds. To perform a well-learnt sequence, its constituent elements are preserved and organized in an orderly fashion through a motor program (Keele et al., 2019; Klapp & Greim, 1979; Lashley, 1951; Sternberg et al., 1978). Equally critical, the role of temporal organization in motor sequence control has been investigated in frontal lobe patients (L. Deecke et al., 1985; Foerster, 1936; Halsband et al., 1993; Kleist, 1907; Nichelli et al., 1995; Picton et al., 2006), and patients with cerebellar (Bares et al., 2007, 2011; Bareš et al., 2012; Broersen et al., 2016; Richard B. Ivry et al., 2002; Raghavan et al., 2016) and other movement disorders involving the cortico-basal ganglia-cerebellar network (Avanzino et al., 2013, 2016; Bernardinis et al., 2019; Harrington et al., 1998; Jones & Jahanshahi, 2014, 2015; Martino et al., 2019), exhibiting disruptive timing in sequential timing behaviors. While volitional movements are prepared before they begin (Ghez et al., 1991; Rosenbaum, 1980), what remains yet unaddressed is how order and timing are represented during sequence planning.

CQ models accounting for the control of serial behavior (Grossberg, 1978a, 1978b; Houghton, 1990) posit that sequential movements are preactivated in parallel and compete with each other in a process to be selected for execution. In the CQ architecture, serial order of movement elements is retained in a planning neuronal map of simultaneous, yet graded, activations which are ranked depending on elements' ordinal position (Farrell & Lewandowsky, 2002, 2004; Grossberg & Pearson, 2008; Page & Norris, 1998; Brown et al., 2000, 2007; Burgess & Hitch, 1992, 1999; Henson, 1998a, 1998b, 1999; Hurlstone & Hitch, 2015, 2018; Lewandowsky & Farrell, 2008). The first direct empirical evidence of a neural code for serial order during sequence planning comes from multi-unit recordings from the prefrontal cortex of trained monkeys in a delay drawing task (Averbeck et al., 2002). The authors found that each sequential movement (stroke) was distinctly associated with a neuronal pattern before sequence execution. During this planning period, the representations of movement-related patterns were co-activated in parallel and ranked by their serial position predicting subsequent correct order during execution. Further, human MEG data have shown that the preparatory queuing pattern of upcoming sequential movements correlated with sequence performance (Kornysheva et al., 2019). Critically, these parallel

patterns were preserved for sequences of different order and timing. Together, these studies advocate for an abstract effector- and timing-independent code for serial order that governs subsequent correct serial execution.

In support of these findings, we have reported a behavioral readout of a preactivation gradient during sequence planning reflecting the ranked availability of movements according to their learnt serial position (Mantziara et al., 2021). It has been suggested that a temporal context may be integrated in the planning map of a CQ mechanism; model simulations suggest that temporal variations operating via overlapping timing signals or oscillators can control the rhythm or temporal grouping of serially recalled items (G. D. A. Brown et al., 2000, 2007; Burgess & Hitch, 1999, 2006; Hartley et al., 2016). This makes the prediction that movements closer in time, as per their perceived timing during learning, would have more similar activations during planning, compromised competition with one another, and thus similar availability states, e.g., comparable RTs and errors (Burgess & Hitch, 1999; Hartley et al., 2016). In the same study, we directly addressed whether temporal proximity of movements is reflected in their availability by investigating the interactive relationship between ordinal position and timing during planning. The position-dependent graded availability of competing movements was found to be invariant of the planned temporal structure or speed of the retrieved sequence. Instead, it linearly expanded with longer preparation time and, when more pronounced, correlated with faster initiation and temporally correct sequence performance. This finding supports two interpretations: First, that movement availability depended on order, not timing, supports the notion that these sequence components may involve two independent processes prior to movement onset (Bednark et al., 2015; Bengtsson et al., 2004; Bortoletto et al., 2011; Kornysheva et al., 2013; Kornysheva & Diedrichsen, 2014; Maslovat et al., 2018; Ullén & Bengtsson, 2003), and, second, the preactivation gradient reflected the quality of sequence plan representation associated with later improved performance.

The capacity to maintain the spatial information of serial order in animal models has been ascribed to frontal cortical activity selective to the ordinal position of to-be-performed sequential actions, in the SMA and pre-SMA (Shima et al., 1996; Shima & Tanji, 2000; Tanji & Shima, 1994), prefrontal cortex (P. Barone & Joseph, 1989; Funahashi et al., 1997; Ninokura et al., 2003, 2004), premotor cortex (Ohbayashi et al., 2003) or widespread in the frontal lobe (Berdyyeva & Olson, 2010). However, this order-related neuronal activity during retrieval or delay periods is reported as intrinsically associated with the temporal order of the intended movements without

investigating a mechanism of how serial order and timing are represented. Therefore, there is a need for establishing any potential dissociation or interaction of a timing and positional signal in the context of a sequence planning mechanism.

Here, we trained healthy participants in planning and executing from memory two unimanual four-finger sequences with identical order but different speeds, slow and fast. We first probed the behavioral availability of constituent movements of the planned sequence by recording RTs and error rates of each ordinal position during a 1.5 s planning period. In keeping with our previous approach (Mantziara et al., 2021), we aimed to establish whether the position-dependent preactivation gradient is modulated by the planned speed of the retrieved sequence. Further, we investigated the planning and execution dynamics over time of the same sequences and a control single press movement. As previously shown with MEG technology (Kornysheva et al., 2019), this was done by using, instead, EEG together with surface EMG for decoding the cortical and muscular activity, respectively. Finally, we reconstructed the cortical activity from the left M1/S1, left PMd, left SMA, right PhG, and the left DLPFC. It is well established that M1 and S1 regions contralateral to the acting hand encode representations of sequential movements during execution (Kornysheva & Diedrichsen, 2014; Yokoi et al., 2018). Although activation in these regions is unlikely to account for abstract representations of orderly movements during sequence planning (Kornysheva et al., 2019), they have been shown to encode effector-specific information (Ariani et al., 2022; Gale et al., 2021). The PMd cortex is one of the regions associated with motor planning activity (Cisek & Kalaska, 2002; Ohbayashi et al., 2003; Pilacinski et al., 2018) encoding the temporal structure of well-trained sequences (Kornysheva & Diedrichsen, 2014; Rossi-Pool et al., 2019). Last, we also examined the left SMA (Berdyyeva & Olson, 2010; Kornysheva & Diedrichsen, 2014; Shima et al., 1996; Shima & Tanji, 2000; Tanji & Shima, 1994), right PhG (Kornysheva et al., 2019) and left DLPFC (Averbeck et al., 2002; Fermin et al., 2016) because of their implication during sequence planning. Decoding at source-level aimed at addressing how these regions contribute to modulations of movement representations during planning and execution depending on ordinal position and sequence speed.

We sought to address how order and timing of the constituent movements are centrally and peripherally represented during the planning and execution periods. According to the CQ prediction, we expected that neural movement-related pattern activations would form parallel traces in a rank order from the 1st to at least the penultimate movement (here, 3rd) whilst converting to serial

order during execution. If the CQ mechanism incorporates a temporal code for sequence timing, here speed, this would be reflected in variable proximity of the parallel traces. In other words, a parallel compression or expansion of parallel movement-related activations would be modulated by the planned speed, following the CQ prediction that closer or overlapping timing signals would render more temporally proximal movements exhibit similar preactivation states (Burgess & Hitch, 1999; Hartley et al., 2016). We predicted that these modulations would not be explained by muscular activity during planning (Kornysheva et al., 2019).

Our behavioral data replicate a graded availability of upcoming movements for accurate and fast production during movement planning depending on their planned ordinal position. In line with previous results (Mantziara et al., 2021), we found that this position-dependent preactivation gradient was not affected by the planned speed. By contrast, EEG decoding revealed no CQ parallel modulation of either ordinal position or speed during planning. Instead, decoded movements were temporally scaled during planning sequences of different speeds, preserving their ordinal position in a serial fashion over time before execution. No such preparatory patterns were observed in the decoded muscular activity of the associated motor presses. Temporal scaling during planning and execution was shared among the regions of interest at source level. Our data suggest that while serial order of upcoming movements becomes competitively organized at the end of planning, a separate, yet co-existing, timing mechanism rehearses their concomitant temporal occurrence by flexibly adjusting the tempo as per the planned sequence speed. This cortically widespread preparatory mechanism is likely to reflect an imprint of timing before execution. This process appears to be supported by critical brain regions that work in concert to create spatiotemporal representations for flexibly controlling timed behavior without compromising order.

3.4 Materials and Methods

3.4.1 Participants

A total of nineteen right-handed Bangor University students participated in the study. After excluding one participant due to excessively noisy EEG data, the data of eighteen participants were analyzed (N = 18; M = 23.5 years, SD = 3 years, 10 females). Hand dominance was assessed with the online Handedness Questionnaire (http://www.brainmapping.org/shared/Edinburgh.php) adapted from the Edinburgh Handedness Inventory (Oldfield, 1971) (N = 18; M = 83.3 %, SD =

16.6 %). Participants had no previous experience in performing a similar motor sequence learning task and were debriefed on the hypothesis of the study only after the completion of the experiment. All participants reported normal or corrected-to-normal vision, normal hearing, and no history of neurological or psychiatric conditions. Study participation followed written informed consent and was compensated with either course credits or £7/h. The recruitment and experimental procedures were approved by the Bangor University School of Psychology Research Ethics Committee (Approval Code 2017-16100-A14320).

3.4.2 Apparatus

During the behavioral training (days 1 and 2) and test (day 3) sessions, participants performed a visually cued motor task on a 19-inch LCD monitor (1280 x 1024 pixels), seated in a quiet dimly lit room while wearing headphones for noise cancellation. The EEG test session (day 4) took place in a dark, sound-shielded Faraday cage where participants performed the task on a 28-inch LCD monitor (1080 x 1920 pixels) with a 100 cm viewing distance to the screen. In both settings, the task stimuli were synchronized with the monitors' refresh rate (60 Hz) and presented with the Cogent 2000 toolbox (v1.29; http://www.vislab.ucl.ac.uk/cogent.php). The experimental visual presentations and response recordings were set up in an in-house MATLAB code (v9.2 R2017a, The MathWorks, Inc., Natick, Massachusetts, United States). Responses were collected from 13 participants using a 5-button fiber optic device (Pyka; Current Designs) throughout the behavioral and EEG sessions. For the rest of the participants (N = 5), responses were obtained from a computer keyboard device in all sessions. A customized foam channeled the devices' cables to prevent movement unrelated to the task and instability. Before task initiation, participants were asked to place the five fingers of their right hand on the specified target buttons of either response device using a wrist cushion.

3.4.3 Behavioral task and experimental design

The task is an adaptation of the delayed sequence production paradigm which has been used to study movement availability during planning of well-learnt movement sequences before execution (Mantziara et al. 2021). To assess sequence or single movement planning and execution from memory, we recorded sequential presses produced with the right index, middle, ring, and

little fingers, single presses with the right thumb, and probe presses with all fingers including the right thumb.

The experiment involved two training sessions, a behavioral test session, and an EEG test session, over four consecutive days (Figure 3.1a). Participants were trained (days 1 and 2) to associate a unique visual cue (abstract fractal shape) with either a four-element finger sequence of the same finger order with a slow or fast speed (*Sequence* trials), or a single press delivered with an unrelated effector to the sequence (*Single press* trials). A trial started with a *Sequence* or *Single press* cue, respectively, which signified the respective required movement and triggered the retrieval of the corresponding target press(es). After a certain delay (1500 ms; preparation period), a *Go* cue prompted the production of the required press(es). In the case of a *Sequence* trial in early training, the *Go* cue (hand stimulus on a gray background) featured timed visual guidance for the target finger sequence by imposing participants to synchronise their presses with the successively displayed digit cues in either of two target rhythms. During training, participants transitioned from visually-guided to memory-guided trials requiring movement production from memory following the *Go* cue (hand stimulus on a green background *without* digit cue(s)), depending on the unique, *Sequence* or *Single press,* cue.

Memory-guided *Sequence* trials assessed production of a slow or fast finger sequence (slow / 800 ms inter-press-intervals, IPIs, fast / 400 ms IPIs; *Speed* condition) in the behavioral test session (day 3; Figure 3.1b). *Single press* trials (control / unrelated effector; *Single press* condition) were of interest in the behavioral session for comparing initiation of a planned single movement as opposed to a whole sequence retrieved and produced from memory. Participants were additionally trained in *Control single press* trials and familiarized with dispersedly presented *Probe* trials. *Control single press* trials (day 3) were always visually guided starting with a unique *Single press* cue and were used for obtaining a behavioral baseline measure of a prepared movement (control / unrelated effector; *Prepared* condition). *Probe* trials (day 3) were designed to assess the preparatory state of constituent movements of the cued sequence (probes for 1st – 4th sequence positions; *Probed position* condition) and that of an unprepared movement, not part of the cued sequence (control / unrelated effector; *Unprepared* condition). A *Probe* trial started with a *Sequence* cue and, following a delay period, a *Probe* cue (single digit cue on hand stimulus) required a fast and accurate press in line with the corresponding displayed digit cue. In the EEG session (day 4; Figure 3.1c), participants underwent memory-guided *Sequence* (slow and fast) and *Single press* trials for

the purpose of decoding the sequential presses and single movement of an unrelated effector, not featuring in the planned sequence, from preparation through to production. As this study set out to assess sequence planning and execution from memory, we present data from the test phases.

For all trial types, participants were instructed to perform the correct target finger press(es) avoiding premature responses (i.e., before the *Go* cue). *Probe*, *Single press*, and *Control single press* trials additionally required participants to respond as fast as possible to the *Go* cue. Instructions for the memory-guided *Sequence* trials emphasized the reproduction of the target finger sequence with a slow or fast speed by adhering to the respective temporal structure as much as possible. Participants received points after each trial with *Sequence* trials followed also by visual feedback enabling them to monitor both their finger and temporal accuracy. The visual feedback and point system have been previously published (Mantziara et al., 2021; pp. 1255 - 1256). *Single press* and *Control single press* trials in that context were treated in the same way as the *Probe* trials.

All visual cues (*Sequence* / *Single press*) at the beginning of a trial had a constant duration of 400 ms followed by a fixation cross displayed for 1100 ms, resulting in a 1500 ms delay. The *Go* cue remained on the screen for 3000 ms in the *Sequence* trials. In the *Probe*, *Single press*, and *Control single press* trials, the *Probe* or *Go* cue, respectively, remained on the screen for 1000 ms. After the end of *Go* / *Probe* cue, a fixation cross and feedback were presented for 1000 ms each. The ITI was 500, 900 or 1300 ms, randomized across trials. A *Sequence* trial had a duration of 4.5 s, and a *Probe* / *Single press* / *Control single press* trial had a duration of 2.5 s (excluding fixation cross and feedback).

For the target finger sequence, different finger order combinations were generated and randomly assigned to each participant. From this pool of sequences, we excluded finger orders with ascending or descending digit triplets. Four additional sequences were introduced as practice sequences in a practice block at the beginning of training. Prior to administration of the test blocks, both behavioral and EEG test sessions started with two training refresher blocks of 37 trials each, containing randomized visually- guided (x 8), memory-guided *Sequence* trials (x 8), *Probe* trials (x 5), visually- guided (x 4), memory-guided *Single press* trials (x 4), and *Control single press* trials (x 8). Each test block consisted of the same number of memory-guided *Sequence* trials for each speed condition. Accordingly, in *Probe* trials each digit (i.e., *Probe*) cue was matched with the *Speed* conditions. Overall, in the behavioral session participants underwent 120 memory-

guided *Sequence* trials per speed condition, 30 *Probe* trials per probed position per speed condition, 30 *Probe* trials for unrelated effector per speed condition, 120 *Single press*, and 120 *Control single press* trials (26 randomly presented trials x 30 blocks: memory-guided *Sequence* x 8, *Probe* x 8 for sequence positions, *Probe* x 2 for unrelated effector, memory-guided *Single press* x 4, *Control single press* x 4). The EEG session involved 128 memory-guided *Sequence* trials per *Speed* condition and 128 *Single press* trials (24 randomly presented trials x 16 blocks: memory-guided *Sequence* x 16, *Single press* x 8).

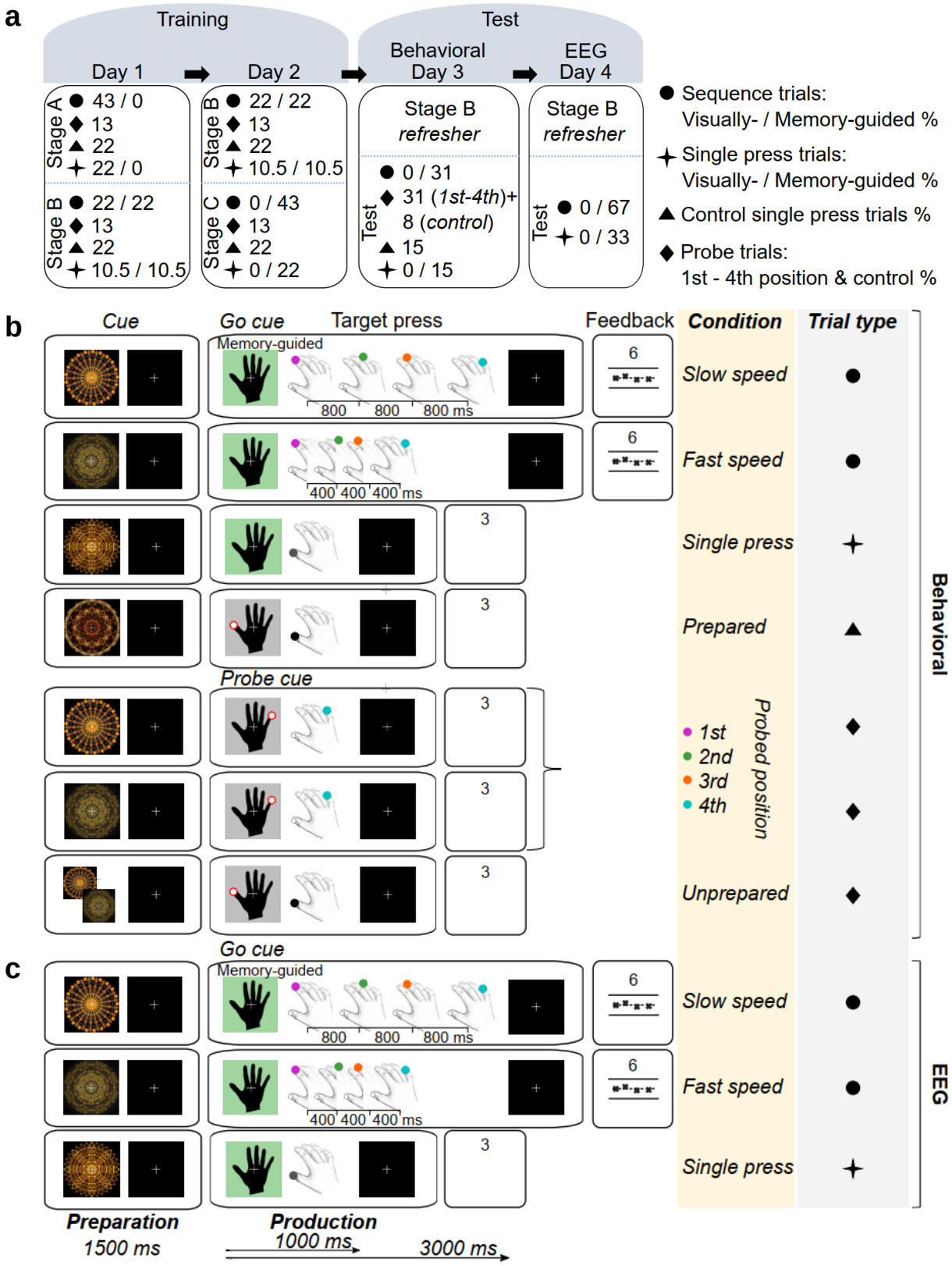

Figure 3.1 | Design, trial types, and experimental conditions. Each trial type is represented with a unique symbol across **a**, **b**, and **c** panels as a cross-reference to corresponding conditions. **a.** Trial types used in training and test

phases are shown in percent of total trials per block. Participants were trained for two days based on a protocol of early (A), intermediate (B), and late (C) training stages. The behavioral test blocks (day 3) contained equal numbers of memory-guided *Sequence* and *Probe* trials, control probes (unrelated effector), and equal numbers of *Control single press* and memory-guided *Single press* trials (see Materials and Methods). The EEG test blocks (day 4) consisted of memory-guided *Sequence* and *Single press* trials. Both test sessions started with a refresher block as the ones used in stage B training. Percentages of *Sequence* trials reflect equal trial numbers for each sequence *Speed* condition. **b.** Behavioral test session: Each sequence *Speed* (memory-guided *Sequence* trials*)* and *Single press* (memory-guided *Single press* trials) condition started with a unique cue and prompted the respective movement production from memory. The *Prepared* condition (*Control single press* trials) commenced with a unique cue and was always visually-instructed (digit cue on *Go* cue). The *Probed position* condition (*1st – 4th* sequence positions) started with a *Sequence* cue signifying a sequence *Speed* condition (slow or fast). **c.** EEG test session: Conditions used were the exact same sequence *Speed* and *Single press* conditions as in the Behavioral test session. For all days and conditions, the preparation period was 1500 ms and the required ('Target') press(es) were as depicted for each condition (**b**, **c**). Bottom arrows represent the duration of a *Go* (3000 ms) or *Probe* (1000 ms) cue display onscreen. After each trial a fixation cross and feedback were displayed (see Materials and Methods).

3.4.4 EEG and EMG acquisition

EEG signal was recorded continuously from 128 scalp (10-20 system) locations using a Biosemi Active II system (BioSemi Instrumentation, Amsterdam, the Netherlands). Concurrently, continuous surface EMG recordings were obtained from eight surface electrodes in a bipolar belly-tendon montage, over the abductor polices brevis (thumb), the abductor digiti minimi (little finger), and the first dorsal interrosei (index) and in a belly-belly montage over the flexor carpi radialis (arm) (Supplemental Figure B.S1 in Appendix B). EEG and EMG data were sampled at 2048 Hz.

3.4.5 EEG and EMG preprocessing

All data preprocessing and subsequent analyses were implemented using the Fieldtrip toolbox (Oostenveld et al., 2011).

EEG and EMG data were trigger-based epoched and filtered applying a Butterworth band-pass filter of 0.5 – 90 Hz with a 4th order high-pass filter and a stopband filter of 48 – 52 Hz for removing line noise.

The EEG epochs were visually inspected for marking noisy trials with very high kurtosis (≥ 40) over large group of channels, indicative of slow drifts, high-frequency bursts in the signal or electronics artifacts (Delorme et al., 2007). Noisy channels were identified via visual inspection in conjunction with the order statistics based outlier detection technique (Giri et al., 2015) (Supplemental Figure B.S2 in Appendix B). This approach is based on detecting outlier channels with

significantly high variability throughout the trial time course using range as a measure of dispersion. Channels with variability above 2 standard deviations from the mean were inspected to avoid marking those channels in which individual trials accounted for any detected maximum variability. On average, 3.1 % of all channels showed consistent noise on a trial-wise basis and excluded from further preprocessing analysis. Data were then re-referenced to average and downsampled to 1000 Hz. The previously detected noisy trials were removed from the data at that stage. Across participants, 4.5 % (range: 0 – 10.2 %) of trials were rejected. Independent Component Analysis (ICA) was performed using blind source separation (Jung et al., 2000) with the implementation of the Infomax algorithm (Bell & Sejnowski, 1995; Shen et al., 2002). Detection and removal of those components accounting for physiological artifacts were guided by inspecting the components' time courses and related topographies. Additional visual inspection of the activity power spectra of each component's frequency course provided a more robust criterion for removing artefactual components driven by EMG noise, whereby decision-making for removal was based on observing a consistently increasing frequency after 5 Hz (Jung et al., 2000) (Supplemental Figure B.S3 in Appendix B). After subtracting the artefactual components and back projecting the data to channel space, the marked noisy channels were interpolated by using the average time-courses of the neighbouring channels located within a 0.13 mm diameter around each problematic channel location and added to the ICA-corrected data. Reconstructing the noisy channels based on ICA-cleaned data overcomes the problem of introducing rank-deficient data and noise to the signal decomposition procedure ensuring a better ICA solution to the EEG data (Nolan et al., 2010).

Preprocessing of the EMG signal after epoching and filtering, included downsampling at 1000 Hz, and rejecting the same noisy trials for each participant as in the EEG data.

3.4.6 EEG source reconstruction

Source reconstruction of the EEG data involved computations for the forward solution based on the standard boundary element method (BEM) volume conductor model of the head (Oostenveld et al., 2003). This method computes the boundary of the solution domain by optimally approximating the three compartments of the head (scalp, skull, and brain) forming closed triangle meshes with the necessary number of boundary elements (nodes) (Fuchs et al., 2001). The BEM model is expressed in Montreal Neurological Institute (MNI) space (in mm) using the geometry of the highly defined *colin27* stereotaxic average brain (Holmes et al., 1998). The template electrode

set of the Biosemi 128 setup, available in the SPM12[5] toolbox (Penny et al., 2007), was aligned to the BEM head model. During re-alignment, the standard fiducials were used as anatomical landmarks (nasion, inion, left and right pre-auricular points) in line with the 10-20 placement system and the electrodes were projected to the nearest points onto the head surface mesh (i.e., the scalp surface). The source model was then constructed creating a dipole 3-D grid with a 7.5 mm resolution by shifting the dipoles inward from the skull by 1 mm for determining the number of dipoles inside the brain volume and the number of dipoles outside. To specify the spatial distribution of the sources (i.e., how activity from a source point reaches the electrodes), the leadfield matrix was computed based on the source model, the head model, and the positions of the re-aligned electrodes.

The inverse solution for computing the spatial filter and estimating the amplitude of the sources was implemented for each participant using a linearly constrained minimum variance beamforming algorithm. This computation was based on the leadfield matrix and the noise-covariance matrix which was estimated from a time window in the baseline period of the baseline-corrected and time-locked preprocessed EEG data. The resulted reconstructed source data were then parcellated for identifying the indices of sources in the tissue corresponding to each of the following regions of interest (ROI): left M1/S1, left PMd, left SMA, right PhG, and the left DLPFC. The parcellation procedure for each region used a 12.5 mm ROI sphere defined via the MarsBar tool of SPM12 in NIFTI[6] format. The ROI masks were created using anatomical MNI coordinates based on previous knowledge on the regions' role in the planning and execution of motor sequences (M1/S1, -22, -36, 52; PhG, 30, -30, -24, Kornysheva et al., 2019; PMd, -24, -15, 58; SMA, -9, 1, 54, Kornysheva & Diedrichsen, 2014; DLPFC, -39, 23, 31, Fermin et al., 2016). Consequently, the ROI-guided parcellation output allowed for creating the ROI source data featuring a binary mask for the dipole positions corresponding to the ROI tissue. Last, the channel (sensor) level data (baseline-corrected and time-locked preprocessed data) were linearly mapped onto the virtual channel level using the spatial filter information from the ROI source data and the

[5] Statistical Parametric Mapping software (https://marsbar-toolbox.github.io/index.html, https://www.fil.ion.ucl.ac.uk/spm/software/spm12/).
[6] Neuroimaging Informatics Technology Initiative file format for storing imaging data (https://nifti.nimh.nih.gov/background).

respective specified ROI dipole positions. This resulted in creating 20 virtual channels for M1/S1, DLPFC, and SMA, 18 for PMd, and 21 for PhG.

3.4.7 Time-frequency representation analysis

EEG signal decomposition at sensor level was conducted for each participant applying Morlet wavelet transform with a constant width of 7 cycles in each frequency for computing the time-frequency values over sliding time windows of 0.1 s. This method was used to extract the power spectra over all sensors or virtual channels between 1 and 80 Hz for correct trials only (see Statistical Analysis) of each movement condition (slow sequence / fast sequence / single press).

3.4.8 Linear discriminant analysis

Preprocessed EEG data at sensor and source level and EMG data were subjected to linear discriminant analysis (LDA) for calculating the probability of the activity pattern of each press condition (1st press position, 2nd press, 3rd press, 4th press, single press) in *Sequence* trials over the whole trial period. The single press pattern was extracted from *Single press* trials which were produced with a finger not featuring in *Sequence* trials (thumb). This condition, therefore, served as a control pattern as it lacked sequential context and had no overlap in effector-specific information.

From the preprocessed data, only correct trials (see Statistical Analysis) were used for classification. The data were baseline-corrected by subtracting the mean activity across 0.5 s prior to the *Sequence* / *Single press* cue for each trial and channel, respectively. A trial-wise (trial-fold) leave-one-out cross-validation was used for the LDA procedure. The mean voltage pattern during a 100 ms window before press onset for each button press from *Sequence* and *Single press* trials, and the common sensor-by-sensor covariance matrix were calculated from the training dataset. We used a Gaussian-linear multi-class classifier to compute the posterior probability of an activity pattern belonging to each of the five press conditions (1st, 2nd, 3rd, 4th press positions, single press) across non-overlapping 100 ms windows along the time course of a *Sequence* trial (including baseline / ITI, preparation, and production periods).

3.4.9 Temporal normalization of pattern probabilities

To probe the presence of temporal scaling or deviation across slow and fast sequence conditions, in a post hoc analysis the press pattern probability curves of the sensor- and source-level EEG data and EMG data were normalized relative to trial-by-trial movement time in the preparation and production periods. Movement time was defined as the time between the onset of the 1st and 4th press in the sequence, corresponding to 0 and 100 % of the movement time, respectively. This was used as the reference time frame for detecting the corresponding probability values in the time series on a trial-by-trial basis. For each participant and sequence condition, probability values were extracted from 50 % of the movement time before the 1st and after the 4th press of the production period time series. To normalize the probability values of the preparation period time series, the *Sequence* cue was taken as the reference time point reflecting the onset of sequence retrieval. Accordingly, probability values were extracted from 50 % of the movement time before the *Sequence* cue and after the end of movement time. The extracted values for both periods were resampled to 200 time points per press pattern. This resampling transformation yielded directly comparable time series for both sequence speed conditions and periods, allowing for testing for the temporal scaling hypothesis based on corresponding time samples. To visualize the motor presses recorded from the behavioral task during the EEG session, we normalized the motor press timings on a trial-wise basis for each participant by calculating the percent timing of each press, using movement onset (i.e., first press) as a reference, relative to movement time (press timing defined as the absolute difference of 1st from 1st, 2nd from 1st, 3rd from 1st, 4th from 1st; each press timing / movement time x 100).

Further, to determine the timing dynamics of the probability peaks, velocity of the normalized press probability values was computed for each participant and condition for establishing the change in position relative to time in each period.

3.4.10 Statistical analysis

Statistical analyses were conducted with the IBM SPSS Statistics v27.0 software (IBM Corp., Armonk, NY) on data acquired from the test sessions (days 3 and 4). In all behavioral analyses involving RT data, only correct trials were included. As correct *Probe* / *Single press* / *Control single press* trials were registered those with a correct digit press and correct number of presses (i.e., one), conducted within 1000 ms from the *Probe* / *Go* cue (*Probe* trials for 1st - 4th: 85 % for

slow, 87 % for fast; *Probe* trials for control: 82 % for slow, 81 % for fast; *Single press* trials in behavioral session: 93 %; *Single press* trials in EEG session: 97 %; *Control single press* trials: 96 %). Correct *Sequence* trials were those with correct digit presses in the correct order and correct number of presses (i.e., four), produced within 3000 ms from the *Go* cue with mean temporal error ≤ 50 % (Behavioral session: 95 % for slow, 91 % for fast; EEG session: 98 % for slow, 97 % for fast). As the same criteria were applied for the trials submitted to LDA, all subsequent statistical analyses of the sensor- and source-level EEG and EMG data were performed on correct trials only of the preprocessed data.

Behavioral data. To assess the availability of each of four movements associated with different sequence positions during planning, we analyzed the raw median RT and mean error rate of *Probe* trials. Specifically, we examined the position-dependent differences by testing for RT and error increases from 1st to 2nd and 2nd to 3rd positions across speed conditions using one-tailed paired samples *t* tests. Since our previous findings (Mantziara et al., 2021) have pointed to an elevated availability of the 4th position compared to the 3rd position, we tested for a decrease in RT and errors from 3rd to 4th position (one-tailed paired samples *t* tests). We were then interested in replicating our hypothesis of an absent effect of sequence speed on movement availability depending on sequence position. To that end, we performed two separate two-way repeated-measures ANOVAs for analyzing RTs and errors, respectively, under the factors Position (1st / 2nd / 3rd / 4th) and Speed (slow / fast).

The availability of an unprepared movement not learnt as part of the cued sequence (control / unrelated effector – *Probe* trials), was tested against the last sequential movement (4th position – *Probe* trials) (unprepared minus 4th position; one-tailed paired samples *t* tests for RT and error rate). We additionally hypothesized that planning a whole sequence would yield a cost reflected in a lower preparatory availability for sequence initiation (1st position – *Probe* trials) as compared to a prepared single movement (control / unrelated effector – *Control single press* trials). Thus, we predicted that a prepared movement would exhibit faster RTs and less errors when contrasted with the 1st sequential movement (1st position minus prepared; one-tailed paired samples *t* tests for RT and error rate).

Further, to probe the association between the preparatory availability state of movements and subsequent sequence performance, for each participant we computed the size of the preactivation gradient by taking the mean relative RT and error difference across 1st-2nd, 2nd-3rd, and

3rd-4th positions in the slow condition (Mantziara et al., 2021). We conducted four one-tailed Pearson's correlations between each of above measures and sequence initiation RT (*Go* cue to first press latency) and relative temporal error (percent mean deviation of relative timing from target timing), as markers of sequence performance. We predicted that participants with larger size of preactivation gradient would be faster in starting the sequence and show higher relative temporal accuracy (Mantziara et al., 2021). Given that participants had to learn a single finger sequence, we did not expect within-sequence condition inter-subject variability in finger accuracy (Mantziara et al., 2021). In addition, the initiation RT and relative temporal error performance measures in the slow condition were subjected to a median split to explore the position-dependent slopes based on high or low initiation RT and temporal error (four mixed ANOVAs; Position x Group).

Analysis of behavioral responses during sequence production was performed separately on data of the behavioral (day 3) and the EEG (day 4) test sessions. Memory-guided *Sequence* trials were used to assess participants' production timing relative to target timing and the three components of sequence performance: sequence initiation RT, relative temporal error, and finger error (calculated as percent trials with incorrect presses including incorrect number of presses and/or incorrect order out of total trials; see Mantziara et al., 2021; Materials and Methods). Of note, finger error rate for the behavioral data of the EEG test session was still calculated out of total trials including those rejected during preprocessing. First, to establish the extent to which participants adhered to the target speed, relative timing (mean percent duration of three IPIs relative to mean produced IPI duration in the slow condition) was calculated for each participant and the mean relative timing (mean across three relative IPIs) was compared between the two sequence speed conditions (slow minus fast; one-tailed paired samples *t* test). Initiation RT was assessed in the sequence speed and single press conditions (memory-guided *Single press* trials) predicting that producing a planned single movement from memory would be faster than initiating a sequence of movements of either speed (one-way repeated measures ANOVA). The effect of sequence speed condition on relative temporal and finger error was tested using separate one-way repeated measures ANOVAs.

Where the assumption of normally distributed error data was violated in either *Probe* or *Sequence* trials, arcsine transformation was performed (Winer et al., 1991) before submitting the data to the ANOVA models and *t* tests.

Neurophysiological data. Statistical analysis of oscillatory activity at sensor level was reduced to the alpha (8-13 Hz) beta (14-30 Hz) power bands. First, we directly tested for event-related desynchronisation (ERD) by extracting mean data in each Band range (alpha / beta), Period (preparation / production), and Movement condition (slow sequence / fast sequence / single press) relative to baseline using one-tailed paired samples *t* tests. We then investigated potential interaction effects between the factors Band, Period, and Movement submitting the same data to a three-way repeated measures ANOVA to unravel the underlying relationships between the levels of interest.

To test for the CQ hypothesis of parallel preactivations of sequential presses during planning, mean probabilities of each press-related pattern (1st – 4th press positions) of EEG and EMG decoded data were extracted from the last 1 s of the preparation period of the slow and fast conditions. These were analyzed in four separate one-way repeated measures ANOVAs. Pairwise comparisons were focused on the 1st – 2nd, 2nd – 3rd and 3rd – 4th press positions differences.

Serial preactivation processing of press-pattern related probabilities by position number (preparation period) and serial order during sequence execution (production period) were tested using the peak velocity timings computed from the EEG and EMG normalized probabilities as the dependent measure. These were analyzed under the press position conditions in each speed condition and period using four separate one-way repeated measures ANOVAs for each modality. As the press-related preactivation of the 4th press position in the slow speed condition exceeded on average the end of the preparation period (occurring at 78 % of movement time; Figure 3.4a, shaded area in *Slow*), we excluded the 4th press pattern probabilities from analysis of the preparatory normalized signal. As such, in the case of a significant main effect of press position, one-tailed paired samples *t* tests were performed between adjacent press positions (Preparation: 2nd minus 1st, 3rd minus 2nd; Production: 2nd minus 1st, 3rd minus 2nd, 4th minus 3rd). Peak velocity timings were also used for testing the hypothesis of temporal scaling during each period, by predicting an absent effect of sequence speed on peak velocity timings per sequence press position. This was assessed with a two-way repeated measures ANOVA (Speed x Position) for each period and modality. A post hoc exploration of a potential weaker temporal scaling in preparation as compared to production involved a three-way repeated measures ANOVA (Period x Speed x Position). Last, to investigate whether the preparatory and production press positions scaled similarly,

we performed one-tailed Pearson's correlations between the sensor-level EEG peak velocity timings (mean across trials) during preparation and those during production for each press position up to the 3rd press position.

Analysis of the peak velocity timings of the source level EEG data aimed at testing the same hypothesis of serial ordering of press positions and temporal scaling in either period. Thus, we accordingly performed four one-way repeated measures ANOVAs, followed by planned one-tailed paired samples *t* tests between adjacent press positions in case of a significant main effect of press position, and two two-way repeated measures ANOVAs (Speed x Position) for each ROI.

Finally, analysis of the decoded single press condition was centered on establishing a similarity between the EEG decoded signals of the single press and 1st press position based on their timing occurrence and peak amplitude. To address this, we first analyzed the peak velocity timing of the single press and 1st press position probabilities time series in each period and speed condition in paired samples *t* tests (two-tailed, Bonferroni-corrected for four tests at $\alpha = .013$; 1st press position minus single press). Similarly, the peak amplitudes (maximum probability value per participant) of the 1st press-related pattern probabilities and single press pattern probabilities were compared with paired samples *t* tests (two-tailed, Bonferroni-corrected for four tests at $\alpha = .013$; 1st press position minus single press) in each period and speed condition.

In the case that the assumption of sphericity was violated in any of the repeated measures ANOVA tests, the degrees of freedom for the *F*-distribution were adjusted using the Greenhouse-Geisser correction (if ε statistic < .75). Reported effect sizes were measured by means of partial eta-squared ratios and standardized mean differences (Cohen's *d*) for the ANOVA and *t* tests, respectively.

3.5 Results

3.5.1 Behavioral data

3.5.1.1 Reaction times and errors during sequence and control movement planning

To examine the behavioral availability of constituent movements at the end of sequence planning, we analyzed RTs and error rates of probed movements (*Probe* trials) recorded for each sequence position 1.5 s after the *Sequence* cue as in Mantziara et al. (2021). Figure 3.2a shows the

percent increases in RT and error rate relative to the first position for each dependent measure (raw RT and press error graphs in Supplemental Figure B.S4 in Appendix B; see Supplemental Table B.S1 in Appendix B for statistics). Planned comparisons were performed to test for position-dependent differences in RT and error increases up to the penultimate position across speed conditions. RT analysis (Figure 3.2a, left) showed a significant increase from 1st to 2nd position [$t(17) = -7.24$, $p < .001$, $d = 1.71$] while the increase from 2nd to 3rd position did not reach significance [$t(17) = -1.45$, $p = .083$, $d = 0.34$]. Press errors (Figure 3.2a, right) revealed a significant increase from 1st to 2nd position [$t(17) = -4.07$, $p < .001$, $d = 0.96$] and 2nd to 3rd position [$t(17) = -1.82$, $p = .043$, $d = 0.43$]. As previous findings have shown a tendency of increased availability for the 4th position compared to the 3rd (Mantziara et al., 2021), we tested for a decrease which reached significance for the errors [RTs: $t(17) = 1.00$, $p = .166$, $d = 0.24$; Error rates: $t(17) = 2.08$, $p = .027$, $d = 0.49$]. Responses to probed positions during planning did not vary by sequence speed as attested by a non-significant interaction between Position and Speed [RTs: $F(3, 51) = 2.14$, $p = .107$, $\eta^2p = .11$; Error rates: $F(3, 51) = 0.48$, $p = .697$, $\eta^2p = .03$]. In sum, while both RTs and errors reliably showed competitive availability between the first two positions, error responses showed a most pronounced graded availability up to the 3rd position. This movement availability was not subject to any variations due to planned sequence speed.

As predicted, probing an unprepared control movement following sequence preparation (Figure 3.2a) which did not feature in the planned sequence resulted in significantly slower [$t(17) = 4.90$, $p < .001$, $d = 1.15$] and more erroneous responses relative to the last probed sequence position [$t(17) = 1.75$, $p = .05$, $d = 0.41$]. By contrast, a prepared single movement (same effector as the unprepared control movement) was produced much faster than the 1st probed position [$t(17) = 22.77$, $p < .001$, $d = 5.37$] and with less errors [$t(17) = 2.58$, $p = .010$, $d = 0.61$]. This shows that while an unprepared single, unrelated movement was less available for fast and correct execution, a prepared one was facilitated indicating a sequence-related cost evident when preparing a whole sequence instead of a single unrelated movement.

Contrary to previous findings (Kornysheva et al., 2019; Mantziara et al., 2021), we failed to find a significant correlation between the size of the preactivation gradient and either sequence initiation RT (relative RT differences: $r = .210$, $p = .202$; relative error differences: $r = -.241$, $p = .167$) or relative temporal error (relative RT differences: $r = .302$, $p = .111$; relative error differences: $r = -.053$, $p = .417$) (see Supplemental Table B.S2 in Appendix B for statistics). Although

participants with faster sequence initiation RT differed significantly from those with slower sequence initiation RT [main effect of Group, $F(1, 16) = 6.19$, $p = .024$, $\eta^2p = .28$], they had no variations in the position-dependent RT gradient [Position x Group, $F(3, 48) = 0.69$, $p = .561$, $\eta^2p = .04$], suggesting that the RT position-dependent differences slope was invariant to sequence initiation RT performance. We found no other significant main effects of Group based on a median split of performance measures for the position-dependent RT and error differences [RT differences: median split of relative temporal error, $F(1, 16) = 0.19$, $p = .668$, $\eta^2p = .01$; Error differences: median split of initiation RT, $F(1, 16) = 0.04$, $p = .844$, $\eta^2p = .00$; median split of relative temporal error, $F(1, 16) = 1.43$, $p = .250$, $\eta^2p = .08$] (see Supplemental Table B.S3 in Appendix B for statistics). These results are likely due to decreased power in opposition to our previous findings which were based on a larger sample ($N = 55$; Mantziara et al., 2021). A post hoc power analysis (G*Power 3.1.9.7, RRID:SCR_013726) showed that the present study was powered at only 34 % to find an effect size as low as 0.30 for the correlations between RT and error differences and performance measures, and at 25 % for the effect size of 0.28 of the main effect of Group based on initiation RT. Therefore, to obtain a medium effect size with at least the same amount of power as previously achieved (i.e., ≥ 72 %), future studies examining such associations should target larger samples ($N \geq 54$).

3.5.1.2 Performance in sequence and single press execution

Following training, finger sequences were produced from memory (days 3 and 4) with high accuracy by sequence speed condition (behavioral session: slow, M = 95 %, SD = 6 %; fast: M = 91 %, SD = 8 %; EEG session: slow, M = 98 %, SD = 2 %; fast: M = 97 %, SD = 3 %). As expected, sequence production was modulated by speed depending on the retrieved sequence as prompted by the *Sequence* cue. Mean relative timing differed significantly at group level between the sequence conditions [behavioral session: $t(17) = 18.36$, $p < .001$, $d = 4.5$; EEG session: $t(17) = 41.73$, $p < .001$, $d = 9.8$] with the fast sequence produced on average in half the time (behavioral session: M = 49 %, SD = 11 %; EEG session: M = 47 %, SD = 5 %) of the slow sequence (behavioral session: M = 100 %, SD = 1 %; EEG session: M = 100 %, SD = 0 %) (Figure 3.2b; d). There was a difference in initiation RT depending on movement condition (slow sequence, fast sequence, single press) [behavioral session: $F(1.26, 21.42) = 263.59$, $p < .001$, $\eta^2p = .94$; EEG session: $F(2, 34) = 18.96$, $p < .001$, $\eta^2p = .53$] with the single press being significantly faster than initiating

either a slow or a fast sequence (behavioral session: $p < .001$; EEG session: $p = .001$) whilst the two sequence conditions did not differ (behavioral session: $p = .216$; EEG session: $p = 1.00$) (Figure 3.2c; e, left). Although participants tended to make slightly more finger errors in the fast sequence condition (Figure 3.2c; e, right) [behavioral session: $F(1, 17) = 7.94$, $p = .012$, $\eta^2p = .32$; EEG session: $F(1, 17) = 7.30$, $p = .015$, $\eta^2p = .30$], relative temporal error was unaffected by speed condition [behavioral session: $F(1, 17) = 0.10$, $p = .756$, $\eta^2p = .006$; EEG session: $F(1, 17) = 0.001$, $p = .974$, $\eta^2p = .00$] (Figure 3.2c; e, middle) (see Supplemental Table B.S4 in Appendix B for statistics).. These findings show that participants were able to retrieve and produce finger sequences of different speeds from memory with equally correct temporal accuracy relative to the target timing. Executing a single movement from memory was faster compared to initiating a sequence of any speed, suggesting a sequence-related cost in initiating the production of a sequence.

Overall, the behavioral results are in line with the previously found preactivation gradient during sequence planning (Mantziara et al., 2021). RTs and errors to movement probes during planning of the respective sequence showed a graded position-dependent availability of sequential movements up to the penultimate position. Contrary to our previous report on producing sequences of different speeds and temporal structure with the same finger accuracy (Mantziara et al., 2021; Figure 2.5b, right, *experiments 2 and 3*), here, participants committed more finger errors in the fast sequence. Despite overlearning a single finger order at two isochronous speeds, it is likely that this difference was the result of a low contextual interference effect which is associated with poorer performance at retention due to decreased cognitive demands during learning (Lin et al., 2010; Magill & Hall, 1990; Pauwels et al., 2014; Shea & Morgan, 1979; D. Wright et al., 2016; D. L. Wright et al., 2004). Importantly, although sequences were produced with correct temporal accuracy matching the target sequence speed, availability of the individual sequential movements during planning was unaffected by the planned speed. Yet, availability of movements appears to differentiate depending on movement type (i.e., sequential *vs* single unrelated movement), with an unprepared unrelated effector being more inhibited when a target sequence is retrieved and prepared. By contrast, a prepared unrelated effector is more facilitated suggesting that planning the constituent movements of a sequence is more demanding.

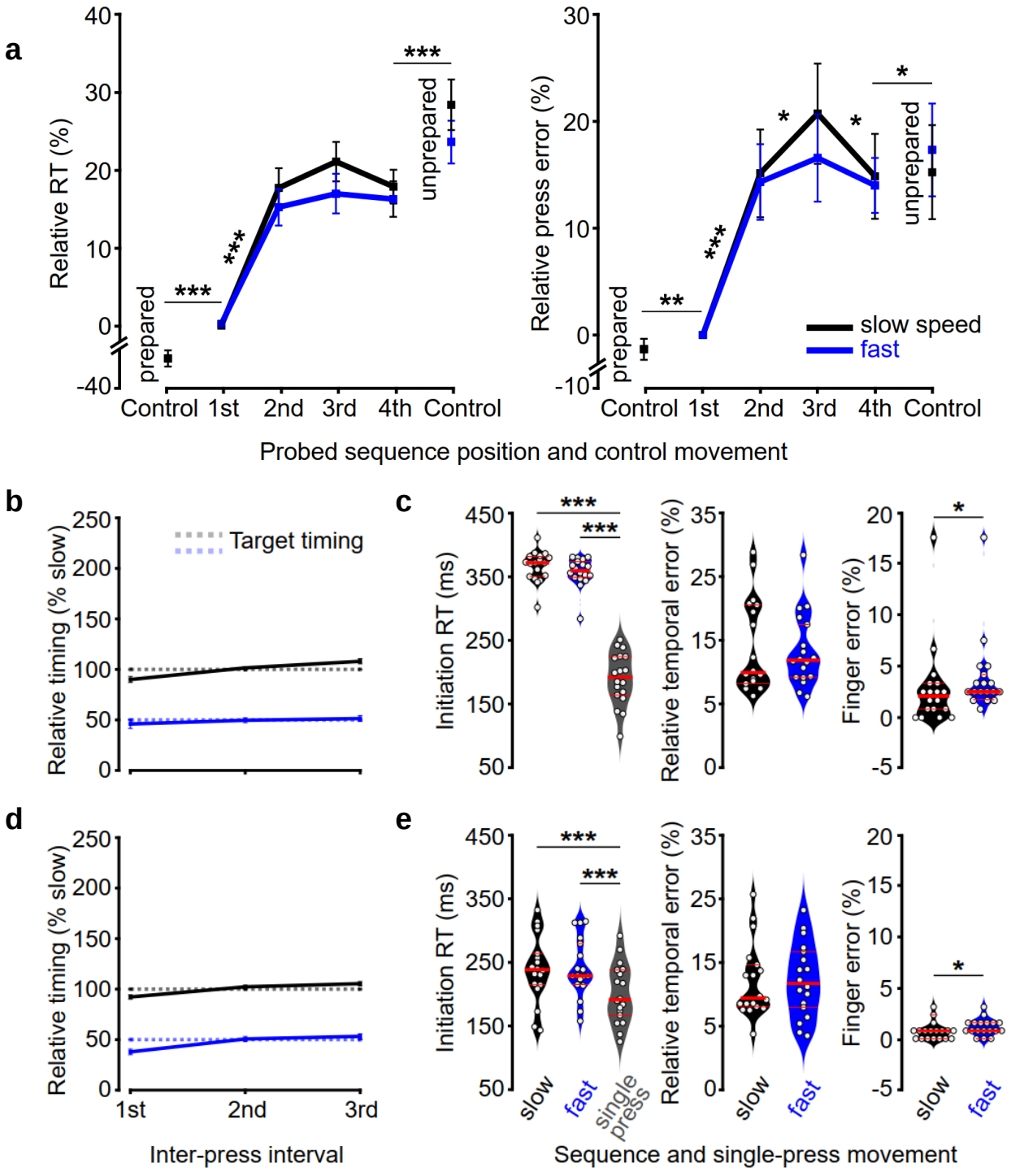

Figure 3.2 | Planning and execution. a. Sequence and control movement planning: Relative RT (left) and relative press error (right) are normalized values relative to first position obtained from *Probe* trials (*Probed position*; *1st – 4th* sequence positions), control *Probe* trials (*Unprepared*), and *Control Single press* trials (*Prepared*) (*cf.* raw RT and press error graphs in Supplemental Figure B.S4 in Appendix B). **b, d**. Sequence production from memory: Relative timing as a function of IPI during production of a slow and fast speed sequence in the Behavioral (**b**) and EEG (**d**) sessions. The produced (solid lines) and target IPIs (dashed lines) were normalized relative to the slow

speed condition. **c, e**. Sequence and single press performance: Initiation RT in each movement type condition (slow / fast sequence, single press), and relative temporal error and finger error during sequence production, as performed from memory in the Behavioral (**c**) and EEG (**e**) sessions. Error bars represent standard errors (**a**, **b**, **d**). Thick red lines represent the median, and lower and upper thin red lines represent the 25th and 75th percentiles, respectively (**c**, **e**). *$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$. RT, reaction time; IPI, inter-press interval.

3.5.2 Neurophysiological data

3.5.2.1 Oscillatory activity

During the EEG session (day 4), participants were prompted to prepare for 1.5 s and produce from memory a temporally distinct isochronous sequence of either speed (slow or fast) or a single press, following a *Go* cue. First, we wished to establish that our task evoked pre- and peri-movement-related oscillatory changes of ERD underpinning the preparation and production of each movement condition. Control analysis of the EEG signal at the time-frequency domain revealed the expected power fluctuations guided by the prevalent beta (14-30 Hz) and μ-alpha (8-13 Hz) rhythms of the sensorimotor circuit (see Supplemental Table B.S5 in Appendix B for statistics). In all movement conditions (Figure 3.3), we found a significant decrease in the beta band for both preparation and production compared to baseline (paired samples *t* test: preparation, slow, $t(17) = 2.66$, $p = .009$, $d = 0.63$; fast, $t(17) = 2.61$, $p = .009$, $d = 0.62$; single press, $t(17) = 1.77$, $p = .048$, $d = 0.42$; production, slow, $t(17) = 3.81$, $p < .001$, $d = 0.90$; fast, $t(17) = 3.95$, $p < .001$, $d = 0.93$; single press, $t(17) = 2.12$, $p = .025$, $d = 0.50$). Although we did not detect significant decrease in the alpha band during preparation (slow, $t(17) = -0.14$, $p = .445$, $d = 0.03$; fast, $t(17) = 0.41$, $p = .342$, $d = 0.10$; single press, $t(17) = -0.13$, $p = .450$, $d = 0.03$), alpha ERD was present during production of a slow or fast sequence but not of a single press (slow, $t(17) = 1.89$, $p = .038$, $d = 0.45$; fast, $t(17) = 2.29$, $p = .018$, $d = 0.54$; single press, $t(17) = 1.56$, $p = .069$, $d = 0.37$). Movement did not interact with Band and Period ($F(4, 68) = 0.65$, $p = .632$, $\eta^2 p = .037$) while post hoc comparisons (Bonferroni-corrected for six tests) of a significant Band x Period interaction ($F(2, 34) = 3.47$, $p = .043$, $\eta^2 p = .170$) confirmed a stronger ERD in the beta band during production compared to baseline ($p = .007$) and preparation ($p = .004$). Overall, these results indicate increased cortical excitation before and during movement execution in the beta power band. Specifically, beta ERD was present during preparation and became stronger during production regardless of sequence speed or movement type (sequential or single). These results are in line with previous

findings reporting decreases in the beta range during movement preparation and execution (Bizovičar et al., 2014; Heinrichs-Graham & Wilson, 2016; Little et al., 2019; Park et al., 2013; E. Rhodes et al., 2018; Sanes & Donoghue, 1993; Schneider et al., 2020; Tatti et al., 2020; Turella et al., 2016; Tzagarakis et al., 2010, 2015). Alpha ERD showed a varying profile as it was detectable during production of a sequence of either speed, suggesting stronger cortical activation during the production of sequential movements than a single movement. At the same time, we did not find significant alpha modulations during preparation of any movement possibly because these changes were calculated across electrodes. Previous studies have reported alpha decreases during movement preparation in central sites of the motor strip (H. Li et al., 2018; Schneider et al., 2020), consistent with the focal sensorimotor origin of the motor-related alpha oscillations (Garcia-Rill, 2015; Gaustaut, 1952; Kropotov, 2016b).

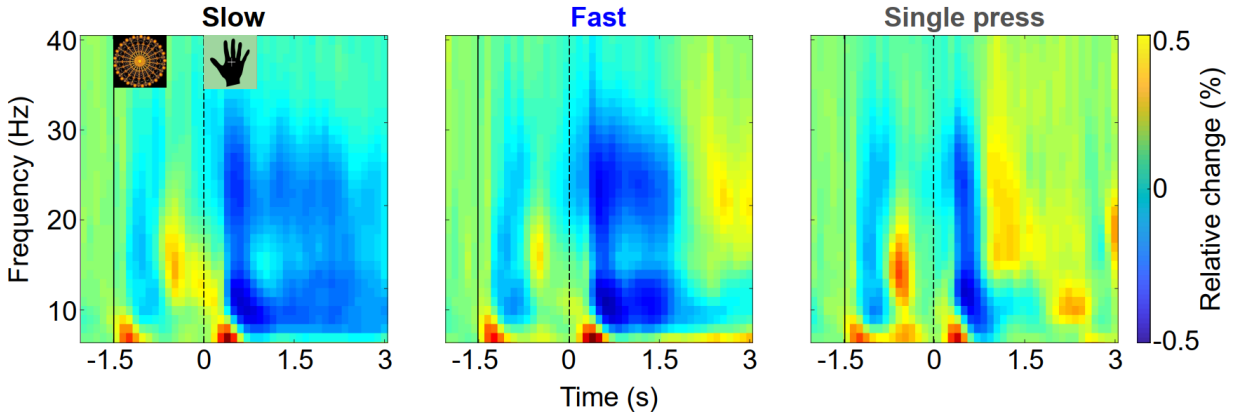

Figure 3.3 | Oscillatory changes in preparation and production. Average time-frequency representation of the EEG activity was computed across electrodes in the alpha and beta frequency range (8-30 Hz) for each movement condition (slow / fast sequence, single press). The solid black vertical line (t = -1.5 s) denotes the beginning of a trial with a *Sequence* or *Single press* cue display (exemplar abstract shape) and of the preparation period up to the display of a *Go* cue (dashed black vertical line at t = 0 s; hand image). The production period started from the *Go* cue to the end of a *Sequence* trial (t = 3 s) or of a *Single press* trial (t = 1 s). Values in color bar reflect percent change of power relative to baseline (0.5 s before the *Sequence* / *Single press* cue); warm colors represent increases; cold colors represent decreases.

3.5.2.2 EEG and EMG decoding at sensor level

Next, we decoded the EEG signal in a trial-by-trial cross-validation approach across the time course of a *Sequence* trial in both speed conditions to calculate the probability of each press-related pattern activation occurring over the preparation and production periods. In addition, we examined whether any observed effects in the preparation period might reflect muscle activation at the periphery. Therefore, the surface EMG data underwent the same LDA decoding procedure.

3.5.2.1.1 EEG decoding shows no evidence of competitive queuing during sequence planning

Previous research in primates (Averbeck et al., 2002) and humans (Kornysheva et al., 2019) has shown that well-trained sequential movements are activated in parallel before sequence initiation consistent with the predictions of CQ models accounting for motor sequence control. We set out to test whether the previously reported neural CQ pattern of preparatory parallel activations would be detectable in the decoded EEG signal during sequence planning and whether it would be modulated by the planned timing, i.e., sequence speed.

If a CQ mechanism controls the planning of sequential elements, we would expect that mean amplitude of the decoded press patterns would be modulated by sequence position with the 1st press position showing higher amplitude than the 2nd and the 2nd press position higher than the 3rd. Additionally, a compression of the parallel preactivations during the planning of a fast sequence compared to a slow one, would indicate that the timing of the planned sequence is integrated within the CQ mechanism. By contrast, we predicted that at the muscular level the decoded EMG press probability pattern for the first press position would be more elevated than for the rest press positions which would not modulate (Kornysheva et al., 2019).

EEG decoding data (Figure 3.4a and b, left) revealed a significant main effect of press position in both conditions during the last 1 s of the preparation period [slow, $F(4, 68) = 53.78$, $p < .001$, $\eta^2 p = .76$; fast, $F(4, 68) = 32.84$, $p < .001$, $\eta^2 p = .66$]. Contrary to our prediction, the mean press-related pattern probabilities were not orderly ranked depending on their position in the sequence: Post hoc pairwise comparisons (Bonferroni-corrected for three tests) showed that mean press pattern probability of the 1st press was significantly lower than the 2nd press ($p < .001$), while 2nd press was not different than 3rd press ($p = 1.000$), and similarly the 3rd press did not differ from the 4th press ($p = .580$). In the fast condition, the mean press pattern probability of the 1st press was significantly lower than the 2nd ($p < .013$) and 2nd lower than the 3rd ($p < .001$),

whereas there was no difference between 3rd and 4th presses (p = 1.000). Analysis of the muscular press patterns (Figure 3.4a and b, right) showed no main effect of press position in either timing condition [slow, $F(4, 68) = 0.78$, $p = .544$, $\eta^2 p = .04$; fast, $F(4, 68) = 0.96$, $p = .437$, $\eta^2 p = .05$] (see Supplemental Table B.S6 in Appendix B for statistics).

These EEG decoding results fail to find evidence for CQ dynamics in sequence planning. Press-related pattern probabilities were not preactivated in parallel and ordered by their position in the sequence. In contrast, we observed rehearsal-like EEG patterns during the whole preparation period resembling the corresponding serial press patterns during the production period.

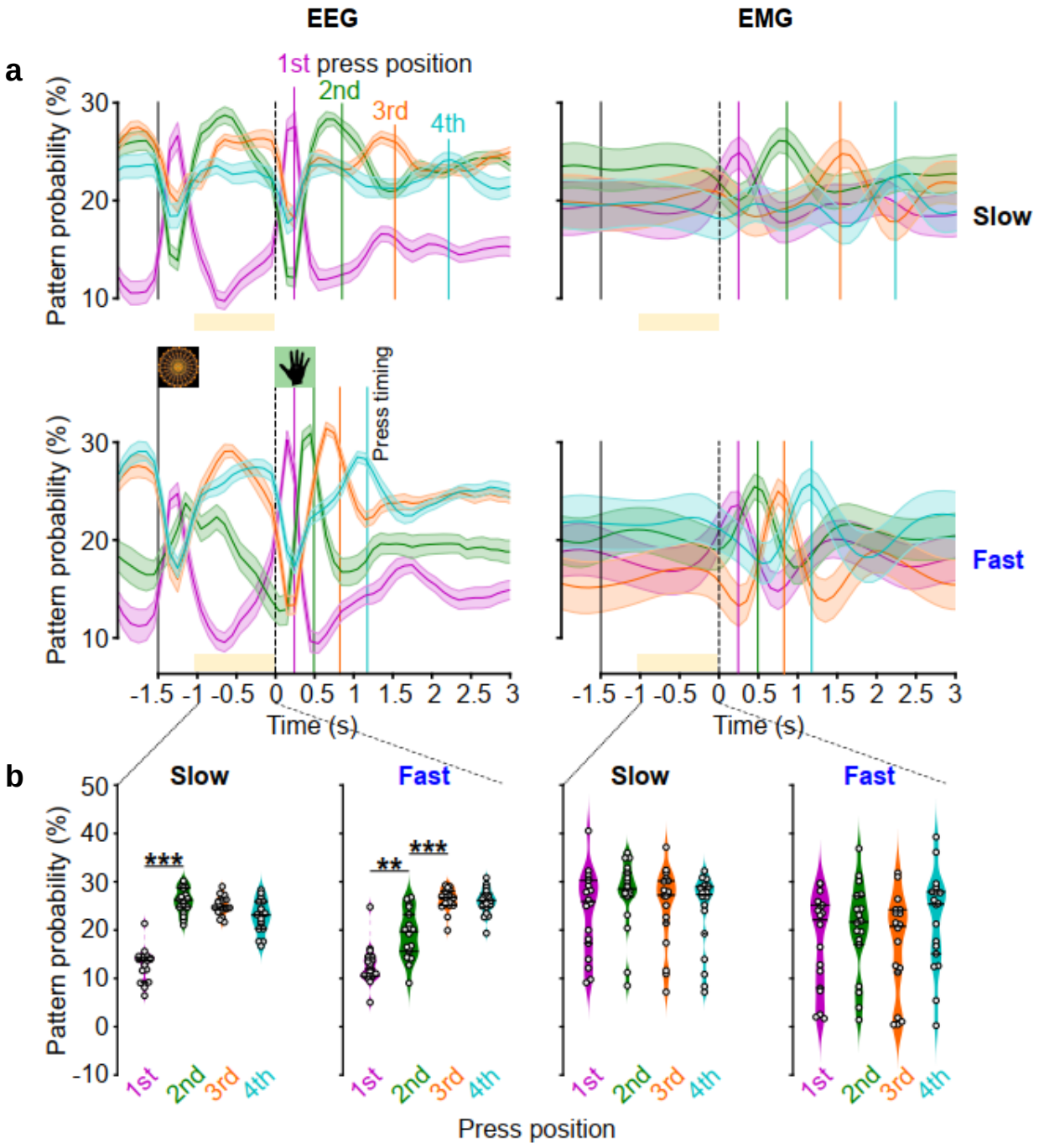

Figure 3.4 | EEG and EMG press-related pattern probabilities. a. Press pattern probabilities of sequential press positions belonging to slow and fast *Sequence* trials were obtained with the LDA decoding procedure for each modality. The classifier was trained in the mean signal across 100 ms before a motor press obtained in *Sequence* and *Single press* trials to distinguish patterns of five classes (i.e., press conditions: 1st, 2nd, 3rd, 4th sequential press positions and a single press). The model then calculated the posterior probability of a pattern belonging to each class over non-overlapping 100 ms time windows across the time series of the signal (i.e., baseline, preparation, and production periods). Shaded areas in trace plots represent standard error. Results for the press pattern probabilities of the single press condition are shown and discussed separately (section *3.5.2.1.3*, Figure 3.6). The exemplar abstract shape (solid black vertical line at t = -1.5 s) at the beginning of a trial denotes the timing of the

Sequence cue display. The hand image (dashed black vertical line at t = 0 s) represents the timing of the *Go* cue display. The interval from *Sequence* to *Go* cue is the preparation period and from *Go* cue to the end of a *Sequence* trial (t = 3 s) is the production period. Press pattern probabilities before the *Sequence* cue belong to a 0.5 s long baseline period. Mean absolute press timing of motor responses for each sequential press position is depicted with vertical color-coded lines after the *Go* cue, averaged across trials. **b.** Mean pattern probabilities for each press position over the last 1 s of the preparation period (bar in ohra across -1 to 0 s in **a**) were calculated for each sequence speed condition and modality to test for differences in the mean amplitude of decoded movements depending on sequential press position (1st – 2nd, 2nd – 3rd, 3rd – 4th). Middle black lines represent the median, and lower and upper black lines represent the 25th and 75th percentiles, respectively. $^{**}p \leq 0.01$, $^{***}p \leq 0.001$. LDA, linear discriminant analysis.

3.5.2.1.2 Sequence-related preparatory activity is temporally scaled depending on planned speed

The acquired EEG preparatory patterns point to preactivation of press-related patterns which are possibly serially rehearsed during the preparation period. First, we examined whether the upcoming sequential presses could be serially preactivated upon sequence retrieval adhering to the serial order of presses in the planned sequence. Second, we sought to unravel the potential role of a planned timing mechanism in the observed EEG and EMG decoded signals. Specifically, we asked whether our task invoked temporal scaling, i.e., slowing down or speeding up the press probabilities during the preparation period depending on the planned sequence condition (slow *vs* fast). To that end, we normalized the time series of the EEG and muscular press probabilities relative to movement time for each condition (see Materials and Methods) (Figure 3.5a). We then calculated the velocity of the temporally normalized press pattern probabilities and computed the timing of peak velocity for each press pattern.

We predicted that scaled EEG peak velocities of press positions would serially ascent over time, i.e., would be temporally ordered, as a function of sequence press position number in either condition or period. In addition, if temporal scaling occurred in both preparation and production periods, the normalized (scaled) timing of EEG peak velocities would be unaffected by sequence condition. If this ordering reflected overt rehearsal at a solely central neural level with no muscular engagement, EMG peak velocities would be ordered and temporally scaled during production but not preparation.

Analysis of the scaled EEG peak velocities showed a main effect of press position in both sequence conditions in preparation [slow: $F(2, 34) = 27.23$, $p < .001$, $\eta^2p = .62$; fast: $F(2, 34) = 67.08$, $p < .001$, $\eta^2p = .80$] and production [slow: $F(2, 34) = 12.20$, $p < .001$, $\eta^2p = .42$); fast: $F(2,$

34) = 15.66, $p < .001$, $\eta^2p = .48$] (see Supplemental Table B.S7 in Appendix B for statistics). Planned comparisons revealed that press positions during preparation were serially ordered in time in both sequence conditions [slow, 2nd minus 1st, $t(17) = 4.62$, $p < .001$, $d = 1.09$); 3rd minus 2nd, $t(17) = 3.12$, $p = .003$, $d = 0.74$; fast, 2nd minus 1st, $t(17) = 4.36$, $p < .001$, $d = 1.03$; 3rd minus 2nd, $t(17) = 9.27$, $p < .001$, $d = 2.18$] (Figure 3.5b, left). Equally, during production press positions were serially ordered in time consistently up to the 3rd press position in the slow condition [2nd minus 1st, $t(17) = 9.96$, $p < .001$, $d = 2.35$); 3rd minus 2nd, $t(17) = 2.22$, $p = .021$, $d = 0.52$; 4th minus 3rd, $t(17) = 1.61$, $p = .063$, $d = 0.38$) and for the whole sequence in the fast condition (2nd minus 1st, $t(17) = 19.14$, $p < .001$, $d = 4.51$; 3rd minus 2nd, $t(17) = 12.75$, $p < .001$, $d = 3.00$; 4th minus 3rd, $t(17) = 13.45$, $p < .001$, $d = 3.17$]. In line with our prediction, timing of scaled EEG peak velocities of press positions did not change significantly depending on sequence condition in either preparation [$F(2, 34) = 3.14$, $p = .056$, $\eta^2p = .16$] or production periods [$F(1.71, 29.13) = 1.35$, $p = .271$, $\eta^2p = .07$] (see Supplemental Table B.S8 in Appendix B for statistics). However, the marginally significant interaction (*cf.* $p = .056$) between press position and sequence speed condition may suggest a less pronounced temporal scaling in preparation. Post hoc pairwise comparisons showed that the timing did not differ between slow and fast sequence conditions (1st press position, $p = .263$; 2nd, $p = .575$; 3rd, $p = .212$, Bonferroni-corrected for three tests). Further, asking whether temporal scaling was less pronounced in preparation compared to production, we explored potential differences in press positions between sequence conditions depending on period (preparation *vs* production). Analysis showed no significant interaction among period, sequence speed condition and press position [$F(2,34) = 1.52$, $p = .233$, $\eta^2p = .08$]. These results indicate that timings of press positions were temporally scaled following the timing of the cued sequence and were serially ordered over time during preparation and during production at least up to the 3rd position.

As predicted, a main effect of press position was found in the scaled EMG peak velocities in the production period of either sequence condition [slow: $F(2, 34) = 14.97$, $p < .001$, $\eta^2p = .47$; fast: $F(1.31, 22.26) = 29.86$, $p < .001$, $\eta^2p = .64$] but not in the preparation period [slow: $F(2, 34) = 1.73$, $p = .192$, $\eta^2p = .09$; fast: $F(2, 34) = 0.98$, $p = .387$, $\eta^2p = .05$] (Figure 3.5b, right) (see Supplemental Table B.S7 in Appendix B for statistics). According to planned comparisons, timing of peak velocities during production was ordered by press position for both conditions [slow: 2nd minus 1st, $t(17) = 3.22$, $p = .003$, $d = 0.76$); 3rd minus 2nd, $t(17) = 2.80$, $p = .006$, $d = 0.66$; 4th

minus 3rd, $t(17) = 2.02$, $p = .030$, $d = 0.48$; fast: 2nd minus 1st, $t(17) = 1.89$, $p = .038$, $d = 0.45$; 3rd minus 2nd, $t(17) = 9.59$, $p < .001$, $d = 2.26$; 4th minus 3rd, $t(17) = 3.62$, $p = .001$, $d = 0.85$]. Timing of scaled EMG peak velocities of press positions during production was invariant of sequence speed condition during production [$F(3, 51) = 1.50$, $p = .226$, $\eta^2 p = .08$], as expected based on the behavioral press timings (Figure 3.5a, insets for timings of 1st-4th press positions) (see Supplemental Table B.S8 in Appendix B for statistics). As predicted, these results suggest that EMG timings of press positions were serially order over time and temporally scaled across speed conditions in the production period only.

Last, we explored whether the timing of scaled EEG peak velocities of each press position during preparation were associated with those during production, across sequence conditions (Figure 3.5c). Pairwise Pearson's correlation analysis showed non-significant relationships for either pair of press positions (1st: $r = .359$, $p = .104$; 2nd: $r = -.291$, $p = .129$; 3rd: $r = .230$, $p = .188$; see Supplemental Table B.S9 in Appendix B for statistics). Of note, correlation analysis for the 1st position was based on fourteen subjects ($N = 14$) after excluding four outlier subjects who accounted for a positive correlation. The above result suggests that timings of press positions did not evolve similarly over time in the preparation and production periods.

Overall, these results demonstrate that neural peak velocities of press pattern probabilities were temporally scaled to match the planned timing of the cued sequence both during preparation and production periods. Peak velocities occurred serially over the preparation time just as during production depending on the learnt serial position of the cued sequence. Although on average the last press position distinctly succeeded the penultimate one as confirmed by the motor press and the EMG timings, the timings of the last two press positions during production of the slow sequence did not differ suggesting possible overlapping timing representations at the central neural level. We did not find any association between preparation and production indicating that timings of press positions did not covary across the two periods. In contrast to the centrally related neural temporal scaling, at the neural periphery there were no increases in press decoding or temporal scaling of those increases during preparation but only during production. This confirms that the preparatory mechanism controlling sequence speed did not reflect overt motor production during the preparation period.

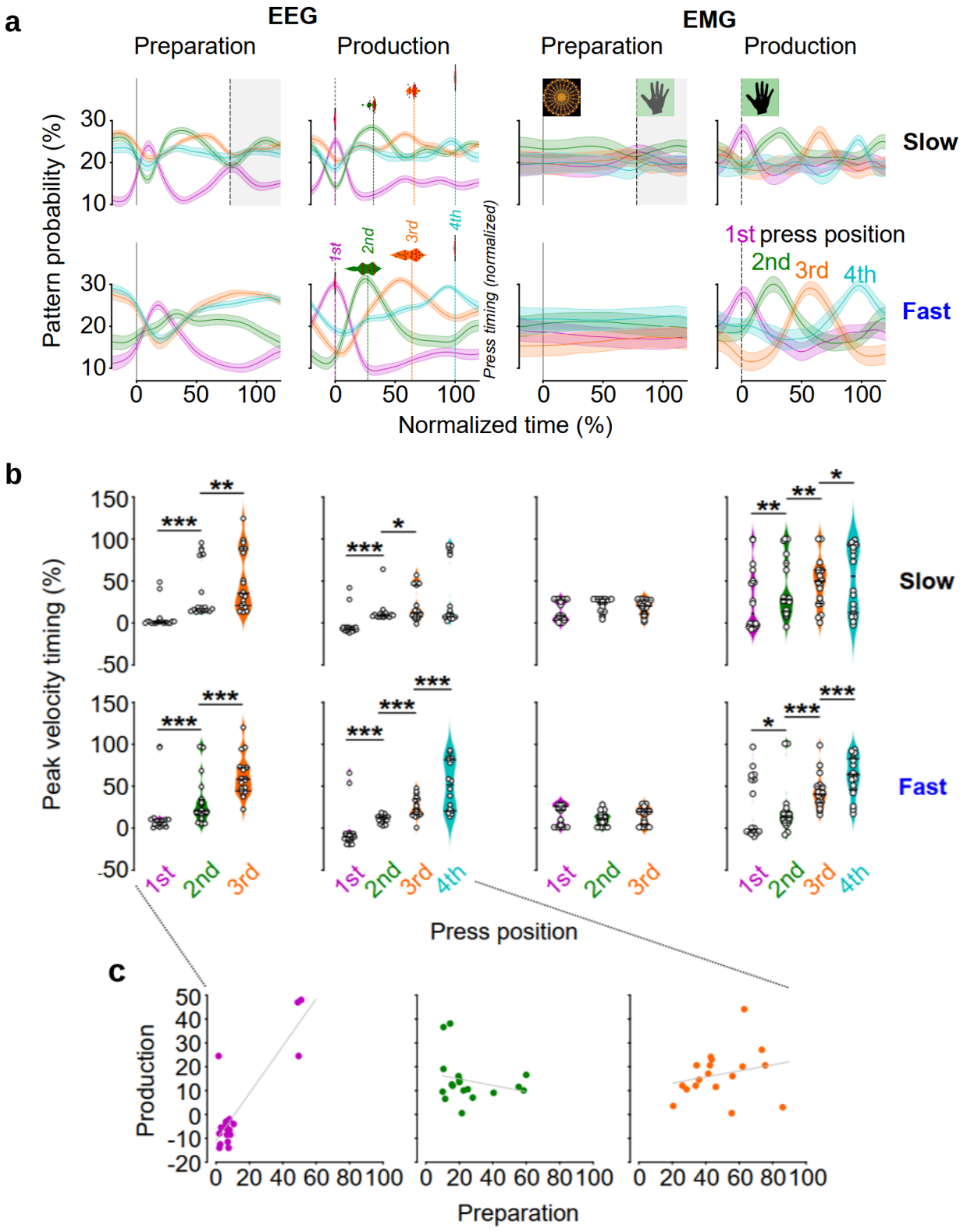

Figure 3.5 | Normalized EEG and EMG press-related pattern probabilities. a. Pattern probabilities directly obtained with the LDA were normalized relative to movement time (i.e., onset of 1st and 4th press in the sequence) and resampled for each period, sequence speed condition, and modality separately. In the 'Production' trace plots,

0 % to 100 % represent movement time. Mean press timings of motor responses were normalized relative to movement time (inset color-coded violin plots). In the 'Preparation' trace plots, 0 % to 100 % represent the onset of sequence retrieval (exemplar abstract shape on solid black vertical line at 0 %) and the end of movement time, respectively. The shaded area in the slow speed condition denotes the end of preparation period at 78 % of movement time (dashed vertical line) and the beginning of production period (shaded hand image signifying the *Go* cue). Shaded areas in trace plots represent standard error. **b.** Mean peak velocity timings of the normalized pattern probabilities as a function of press position. Violin plots follow the columnar organization from (**a**). Data of the 4th press position in the preparatory normalized probabilities were not included in the analysis. Middle black lines represent the median, and lower and upper black lines represent the 25th and 75th percentiles, respectively. **c.** Color-coded pairwise correlations for the peak velocity timings of 1st, 2nd, and 3rd press positions between preparation and production. Each dot represents a participant. $*p \leq 0.05$, $**p \leq 0.01$, $***p \leq 0.001$. LDA, linear discriminant analysis.

3.5.2.1.3 Single press-related activity reflects a high-level timing code at the EEG level

We observed that the single press EEG pattern peaked at the same time as the first press position of the planned sequence (Figure 3.6, left). We assessed this co-occurrence by extracting and comparing the timing of peak velocities for each press pattern and speed condition. Results confirmed that the timings of the 1st press position and the single press coincided in both preparation [1st press position minus single press; slow, $t(17) = -0.60$, $p = .560$, $d = 0.14$); fast, $t(17) = -0.45$, $p = .658$, $d = 0.11$] and production periods [slow, $t(17) = -1.31$, $p = .208$, $d = 0.31$; fast, $t(17) = -1.63$, $p = .122$, $d = 0.38$; Bonferroni-corrected for four tests at $\alpha = .013$]. In addition, the EEG single press pattern exhibited a similar probability to the 1st press (i.e., > 22 % on average). Comparison of the peak amplitudes showed that the single press pattern did not differ significantly from the 1st press position pattern in both speed conditions and periods except for the fast condition in production [preparation: slow, $t(17) = 2.46$, $p = .025$, $d = 0.58$); fast, $t(17) = 1.34$, $p = .197$, $d = 0.32$; production: slow, $t(17) = 2.45$, $p = .026$, $d = 0.58$); fast, $t(17) = 3.76$, $p = .002$, $d = 0.89$; Bonferroni-corrected for four tests at $\alpha = .013$] (see Supplemental Table B.S10 in Appendix B for statistics). The peak amplitude similarity and temporal proximity of the single press pattern to the first press position of a sequence - both occurring around the same time after the *Sequence* and *Go* cue - indicates that the classifier distinguished a single press pattern activation that resembled the first press position activation in both preparation and production periods. Such similarity was not observed in the EMG decoded signal (Figure 3.5, right). Instead, here, as expected, only a motor press associated with the first press position showed an increased probability at the muscular level after the *Go* cue. Therefore, the temporal co-occurrence of similar EEG patterns at the central neural level indicates that the first sequence position and a single movement, which involved a

different effector, likely shared a common abstract code for timing during preparatory rehearsal and movement generation.

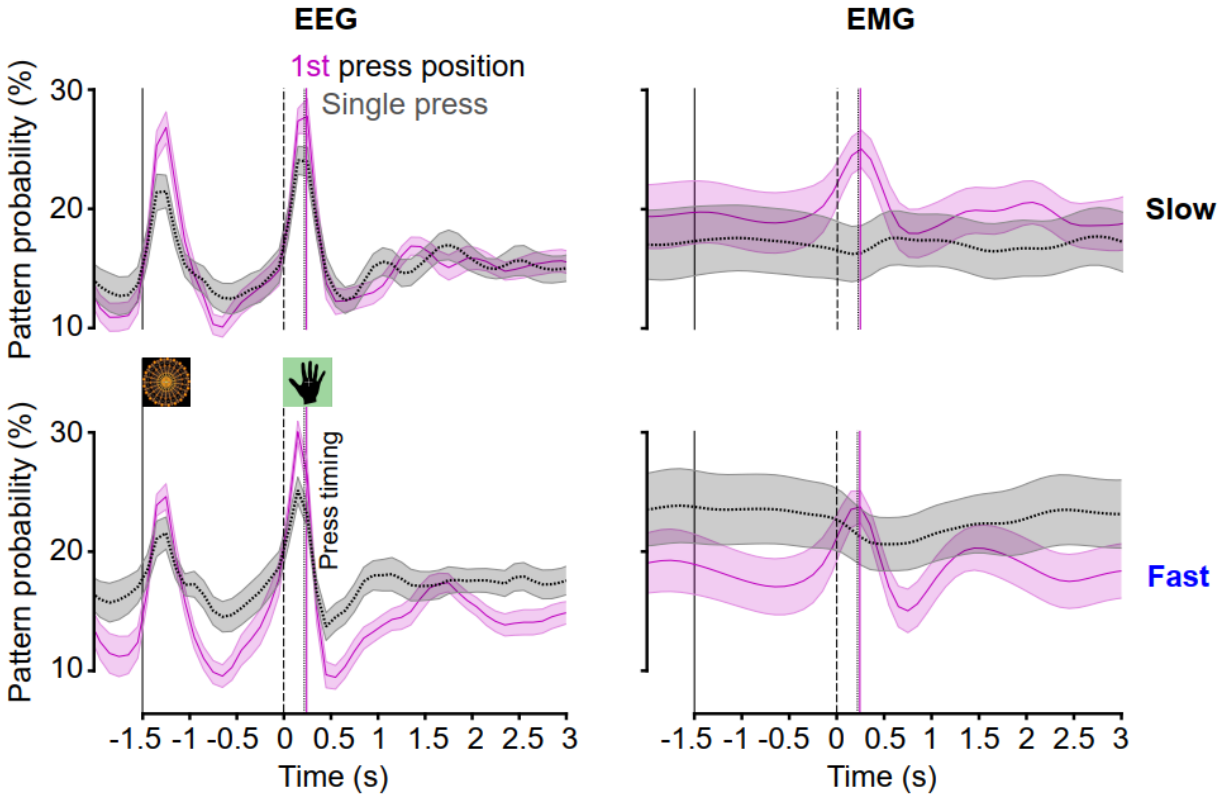

Figure 3.6 | EEG and EMG single press-related pattern probabilities. a. Press pattern probabilities of a single press are shown alongside those of a first press position for each sequence speed condition and modality. Shaded areas in trace plots represent standard error. For a full description of depicted symbols in the graphs, see Figure 3.4a.

3.5.2.3 EEG ROI-based decoding activity at source level

Whole-brain analysis of the normalized press patterns at sensor level showed that presses of a planned sequence were temporally scaled during planning matching the intended sequence speed that occurred subsequently during sequence execution. We aimed to explore the neural sources of temporal scaling examining how brain areas that have been associated with motor sequence planning and production contribute to this process during preparation alone, during pro-

duction alone, or others both. To that end, we reconstructed the EEG data and created virtual channels of ROIs at source level. Identical to the sensor-level analysis approach, the source data underwent the LDA decoding procedure, followed by temporal normalization, and peak velocity timing calculations of the press probabilities. We analyzed the source data from the left M1/S1, left PMd, left SMA, right PhG, and left DLPFC (see Supplemental Table B.S11 in Appendix B for statistics).

All regions of interest (Figure 3.7) showed a main effect of press position, i.e., serial order of timing of peak velocities ascending by press position during the preparation period in both conditions [M1/S1 - slow, $F(2, 34) = 43.81$, $p < .001$, $\eta^2p = .720$; 2nd minus 1st, $t(17) = 4.88$, $p < .001$, $d = 1.15$); 3rd minus 2nd, $t(17) = 4.98$, $p < .001$, $d = 1.17$; M1/S1 - fast, $F(2, 34) = 62.94$, $p < .001$, $\eta^2p = .79$; 2nd minus 1st, $t(17) = 6.97$, $p < .001$, $d = 1.64$; 3rd minus 2nd, $t(17) = 4.06$, $p < .001$, $d = 0.96$; PMd - slow, $F(2, 34) = 50.32$, $p < .001$, $\eta^2p = .75$; 2nd minus 1st, $t(17) = 3.96$, $p < .001$, $d = 0.93$); 3rd minus 2nd, $t(17) = 7.18$, $p < .001$, $d = 1.69$; PMd - fast, $F(2, 34) = 39.93$, $p < .001$, $\eta^2p = .70$; 2nd minus 1st, $t(17) = 4.38$, $p < .001$, $d = 1.03$; 3rd minus 2nd, $t(17) = 5.08$, $p < .001$, $d = 1.20$; SMA - slow, $F(2, 34) = 33.76$, $p < .001$, $\eta^2p = .67$; 2nd minus 1st, $t(17) = 4.37$, $p < .001$, $d = 1.03$); 3rd minus 2nd, $t(17) = 4.07$, $p < .001$, $d = 0.96$; SMA - fast, $F(2, 34) = 51.70$, $p < .001$, $\eta^2p = .75$; 2nd minus 1st, $t(17) = 4.61$, $p < .001$, $d = 1.09$; 3rd minus 2nd, $t(17) = 6.25$, $p < .001$, $d = 1.47$; PhG - slow, $F(2, 34) = 58.28$, $p < .001$, $\eta^2p = .77$; 2nd minus 1st, $t(17) = 5.45$, $p < .001$, $d = 1.28$); 3rd minus 2nd, $t(17) = 5.47$, $p < .001$, $d = 1.29$; PhG - fast, $F(2, 34) = 65.09$, $p < .001$, $\eta^2p = .79$; 2nd minus 1st, $t(17) = 5.86$, $p < .001$, $d = 1.38$; 3rd minus 2nd, $t(17) = 5.78$, $p < .001$, $d = 1.36$; DLPFC - slow, $F(2, 34) = 48.09$, $p < .001$, $\eta^2p = .74$; 2nd minus 1st, $t(17) = 5.91$, $p < .001$, $d = 1.39$); 3rd minus 2nd, $t(17) = 4.39$, $p < .001$, $d = 1.03$; DLPFC - fast, $F(2, 34) = 21.26$, $p < .001$, $\eta^2p = .56$; 2nd minus 1st, $t(17) = 3.00$, $p < .001$, $d = 0.71$; 3rd minus 2nd, $t(17) = 4.67$, $p < .001$, $d = 1.10$].

During the production period, a main effect of press position was found only for M1/S1 in the slow condition, and PhG and DLPFC regions in the fast condition [M1/S1 - slow, $F(2, 34) = 7.84$, $p = .002$, $\eta^2p = .32$; 2nd minus 1st, $t(17) = -0.76$, $p = .229$, $d = 0.18$); 3rd minus 2nd, $t(17) = 4.38$, $p < .001$, $d = 1.03$; 4th minus 3rd, $t(17) = -1.26$, $p = .112$, $d = 0.30$; M1/S1 - fast, $F(2, 34) = 1.64$, $p = .208$, $\eta^2p = .09$; PMd - slow, $F(1.33, 22.66) = 3.56$, $p = .062$, $\eta^2p = .17$; PMd - fast, $F(1.34, 22.83) = 1.63$, $p = .212$, $\eta^2p = .09$; SMA - slow, $F(2, 34) = 0.03$, $p = .968$, $\eta^2p = .002$; SMA - fast, $F(2, 34) = 1.69$, $p = .199$, $\eta^2p = .09$; PhG - slow, $F(2, 34) = 0.01$, $p = .990$, $\eta^2p = .001$; PhG - fast, $F(1.27, 21.54) = 5.53$, $p = .008$, $\eta^2p = .25$; 2nd minus 1st, $t(17) = -2.81$, $p = .006$, $d = 0.66$;

3rd minus 2nd, $t(17) = 2.76$, $p = .007$, $d = 0.65$; 4th minus 3rd, $t(17) = 1.74$, $p = .050$, $d = 0.41$; DLPFC - slow, $F(1.26, 21.35) = 2.29$, $p = .117$, $\eta^2p = .12$; DLPFC - fast, $F(2, 34) = 8.14$, $p = .001$, $\eta^2p = .32$; 2nd minus 1st, $t(17) = -3.36$, $p = .002$, $d = 0.79$; 3rd minus 2nd, $t(17) = 4.37$, $p < .001$, $d = 1.03$; 4th minus 3rd, $t(17) = 0.53$, $p = .301$, $d = 0.13$].

In addition, no region showed a significant interaction between timing of peak velocities and sequence condition in preparation [M1/S1, $F(2, 34) = 1.24$, $p = .302$, $\eta^2p = .07$; PMd, $F(2, 34) = 0.57$, $p = .571$, $\eta^2p = .04$; SMA, $F(1.48, 25.21) = 0.39$, $p = .680$, $\eta^2p = .02$; PhG, $F(2, 34) = 0.26$, $p = .776$, $\eta^2p = .02$; DLPFC, $F(2, 34) = 0.34$, $p = .716$, $\eta^2p = .02$]. Similarly, timings of peak velocities did not differ depending on sequence condition during production [M1/S1, $F(3, 51) = 0.32$, $p = .812$, $\eta^2p = .02$; PMd, $F(3, 51) = 0.48$, $p = .645$, $\eta^2p = .03$; SMA, $F(1.96, 33.40) = 0.39$, $p = .679$, $\eta^2p = .02$; PhG, $F(3, 51) = 2.35$, $p = .084$, $\eta^2p = .12$; DLPFC, $F(3, 51) = 0.52$, $p = .608$, $\eta^2p = .03$].

Altogether, this analysis indicates that temporal scaling of peak velocities timings was present in all regions during preparation and production. However, while serial order by ordinal position was observed consistently in preparation, timings of press positions in production varied or showed weak successions in time, suggesting stronger timing representations of decoded movements during preparation.

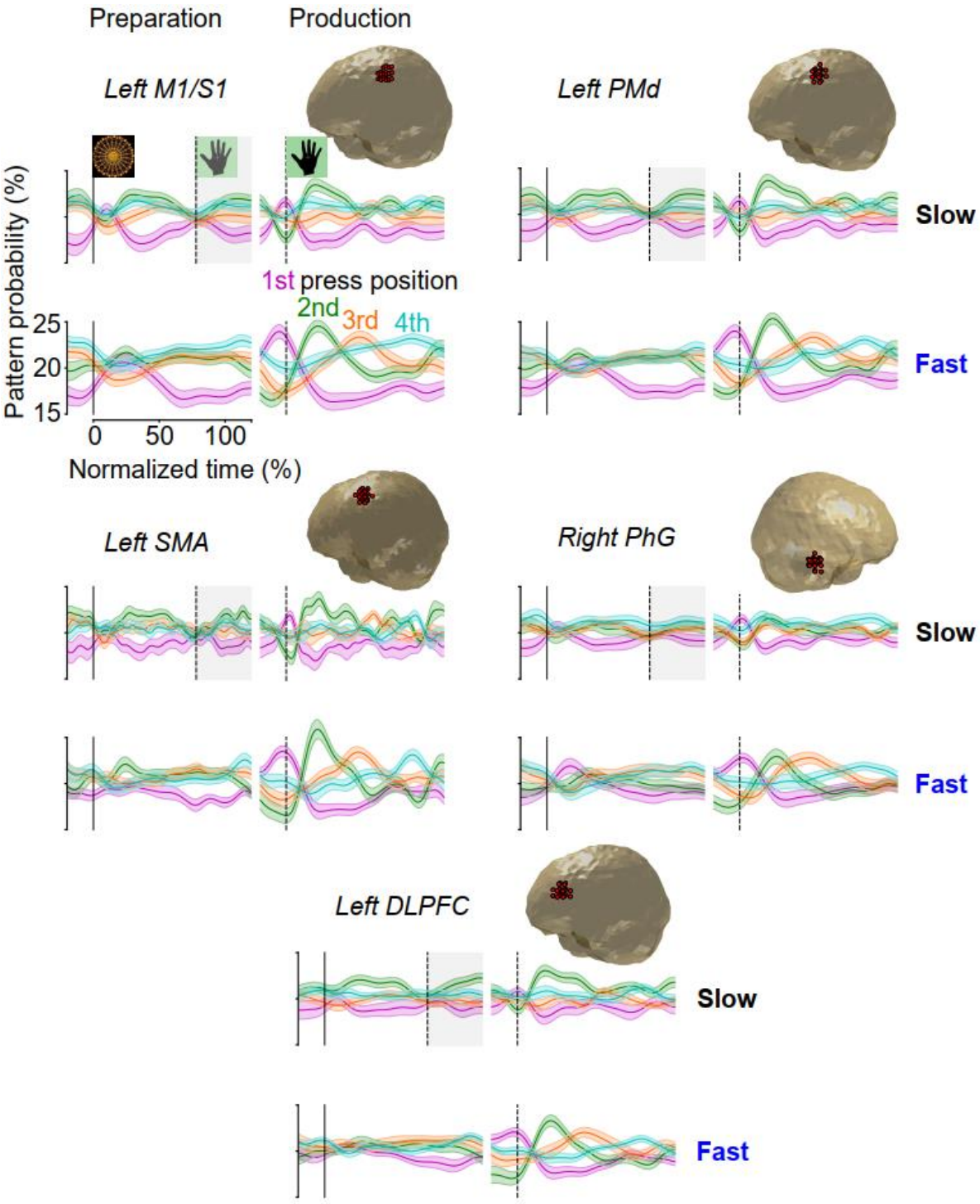

Figure 3.7 | Normalized EEG press-related pattern probabilities at source level. Press-related pattern probabilities of the decoded source-reconstructed signal of five ROIs (left M1 / S1, left PMd, left, SMA, right PhG, left DLPFC) were normalized and resampled for each period and sequence speed condition, following the same calculations as for the press-related pattern probabilities at sensor level (*cf*. Figure 3.5a). Each head model features the volumetric binary mask for the dipole positions corresponding to the tissue of the labelled ROI (see Materials and Methods). Shaded areas in trace plots represent standard error. For a full description of depicted symbols in the graphs, see Figure 3.5a. ROI, region of interest; M1 / S1, primary motor / primary somatosensory cortex; PMd,

dorsal premotor cortex; SMA, supplementary motor area; PhG, parahippocampal gyrus; DLPFC, dorsolateral prefrontal cortex.

3.6 Discussion

This study set out to investigate how serial order and timing are represented during sequence planning. To that end, we trained our participants in planning and producing from memory finger sequences of the same digit order in a slow and fast speed. In line with previous behavioral findings, we show that while upcoming movements are organized in a preactivation gradient and competitively queued by their ordinal position, sequence timing, here speed, is not part of this behavioral CQ code for serial order. Decoding the cortical EEG signal in sequence preparation and production, we demonstrate that movement-related activity is temporally scaled during sequence planning and execution matching the speed of the planned sequence on a trial basis while preserving serial order in time. The temporally scaled preparatory patterns were not accounted for by muscular or effector-related activity. Instead, performing source reconstruction we find that this centrally controlled timing mechanism is distributed across key cortical regions.

Previous findings have shown that sequential movements are prepared in parallel and competitively queued before execution with this preparatory pattern reflecting effector- and timing-independent representation of ordinal position (Averbeck et al., 2002; Kornysheva et al., 2019; Mantziara et al., 2021). In convergence with our previous report (Mantziara et al., 2021), our behavioral results corroborate that upcoming movements occupying a position in a learnt sequence are simultaneously preactivated but in a competitive fashion graded by their ordinal position. This finding is in line with the positional encoding mechanism in sequence production simulations of context-based positional CQ models (Henson, 1998a, 1998b, 1999; Hurlstone & Hitch, 2015, 2018; Lewandowsky & Farrell, 2008). In such systems, the primacy gradient of preactivated plan representations in the planning layer of the CQ architecture dynamically changes over sequence generation receiving input from a positional representation code forming item-position associations. Our data suggest that during sequence learning movements were associated with their respective ordinal positions via Hebb repetition and learning (Attneave & Hebb, 1950; Burgess & Hitch, 1999; Cumming et al., 2003; Hebb, 1961; Page & Norris, 2009). As such, during preparation

participants retrieved sequential elements based on their initially learnt ordinal position as shown by the position-dependent preactivation gradient.

In keeping with our previous findings (Mantziara et al., 2021), although participants were able to correctly modulate sequence execution by the target speed (Figure 3.2b, d), this modulation was not present in the preactivation gradient (Figure 3.2a). These invariant position-dependent differences to the planned sequence speed indicate an absent association between a positional and timing code as part of the CQ mechanism. This finding is at odds with the prediction made by prominent time-based CQ models (Burgess & Hitch, 1999, 2006; Hartley et al., 2016) that an integrated timing signal controls the positional state of elements and their preactivation level depending on their temporal proximity. However, such a functional independence of ordinal position from timing is in line with prior behavioral (Kornysheva et al., 2013; Maslovat et al., 2018; Ullén & Bengtsson, 2003), EEG (Bortoletto et al., 2011) and neuroimaging findings (Bednark et al., 2015; Bengtsson et al., 2004; Kornysheva & Diedrichsen, 2014) advocating different control systems for the preparation of timing compared to order, and a modular control allowing flexible handling and combination of spatiotemporal sequences.

Our data of decoded EEG cortical activity revealed that movements were serially preactivated by ordinal position exhibiting temporal rehearsal that followed the speed of the respective planned sequence (Figure 3.5). To our knowledge, this is the first neurophysiological demonstration in humans of a temporally scaled motor sequence rehearsal or replay during planning. Temporal scaling is best accounted for by dynamic neural patterns that consistently ramp at different speeds (de Lafuente et al., 2022; Mello et al., 2015; J. Wang et al., 2018) or neural population clocks (Coull et al., 2011; Paton & Buonomano, 2018). Our finding of scaled temporal processing during planning and execution may be related to ramping cortical activity typically invoked in timing tasks as shown in the mammalian brain (Ding, 2015; Donnelly et al., 2015; Merchant et al., 2011; Merchant & Averbeck, 2017; Narayanan & Laubach, 2009; Parker, 2016; Parker et al., 2014; Perez et al., 2013; Wang et al., 2018; Zarco et al., 2009). Previous findings from monkeys performing an interval reproduction task confirm that delay-related ramping activity occurring during interval perception could predict activity in a subsequent reproduced time interval (Jazayeri & Shadlen, 2015). In our paradigm, such climbing dynamics, compressed or stretched, according to the intended motor IPIs may explain the scaled peak timings observed during a delay of 1.5 s before movement initiation. It is unlikely that this preparation period acted as a 'temporal receptive

window' affecting subsequent scaled production (Lerner et al., 2014) as no temporal guidance was present in any sensory form. In addition, that this modulation was absent at the muscular space further suggests that a motor timing rehearsal may have operated at the central neural level without motor output. Most importantly, we were able to decode a single movement at a similar timing to the first position of a sequence during preparation and production. These temporally coincident EEG decoded patterns of the single movement and first sequence position (Figure 3.6) point to an effector-independent representation of timing at the beginning of preparatory rehearsal and at movement initiation. Thus, our time-based task may have involved dedicated time representations during sequence learning, allowing participants to rhythmically rehearse the target sequence without overt motor behavior. Such an interpretation is consistent with recent neurophysiological evidence from nonhuman primates for scaled neural oscillatory activity supported by a putative internalized metronome during pre-movement periods; activity mainly in the SMA followed by parietal areas encoded the temporal information allowing this mechanism to flexibly adjust to the timing requirements of the task (de Lafuente et al., 2022).

Contrary to our prediction, we did not observe the previously reported parallel CQ of press-related neural patterns obtained with multi-unit (Averbeck et al., 2002) and MEG (Kornysheva et al., 2019) recordings, despite the complete alignment of probability patterns during production across studies (Figure 3.4). This discrepancy may be due to differences in task affordances. Here, participants had to focus on timing rather than the pre-ordering of movements. In contrast to previous studies, sequences produced from memory retained the same movement order, but required a change in sequence speed on a trial-by-trial basis. This may have manifested itself in the observed scaled preparatory EEG patterns as a temporal adjustment of the movement sequence, i.e., speeding up or down, according to the target, slow or fast, speed. Differences in sensitivity of modalities to source orientations may also account for this diverging result. Scalp EEG recordings are more sensitive to both radial (gyri) and tangential (sulci) source components of cortical activity (with radially oriented dipoles dominating more the EEG signal), whilst MEG detects only tangential sources (Ahlfors et al., 2010; Cohen & Halgren, 2003; Singh, 2014). Nevertheless, a CQ parallel pattern of serial order was observed at the behavioral level, suggesting that this process was retained, but not picked up at the EEG level.

Our results pose the intriguing question of how the CQ-compatible position-dependent pre-activation gradient which we find at the behavioral level can be reconciled with the temporally

scaled EEG pattern replay during preparation. The presence of a behavioral CQ code for serial order may be attributed to certain aspects of preparatory availability that RTs and errors reflect. Our behavioral results ascertain that our task captured this behavioral readout of degree of readiness (RTs; Boardman & Bullock, 1992) and activation strength (errors; Averbeck et al., 2002) as a proxy of movement preactivation level driven by ordinal position. At the same time, the EEG signal detected a putative motor timing engram sensitive to sequences reactivated at the target timescales during preparation. How these two planning mechanisms may collaborate or interact is unaddressed here. We argue that our preparatory scaling results constitute a high-level timing readout of traces of the retrieved sequential movements from intermediate-term memory/LTM at a speed close to the one that they were initially experienced and encoded. A plausible scenario would be that serial order information carried via the CQ mechanism is fed by the organization of temporal interval dynamics depending on the encoded sequence timing (e.g., 400-800-400 ms) to ensure that movement outputs are temporally separated by the input timing. Such an operation would presume a modular control - and possibly a hierarchy (de Lafuente et al., 2022) - of spatiotemporal sequence planning where the CQ module would give order-related input to the timing module or *vice versa*. A future study using concurrent EEG-MEG with various target spatiotemporal sequences would shed light on the presence of a position-driven CQ parallel preactivation pattern at the neural level and a simultaneous motor timing engram during the planning of sequences of different effectors, speeds, and temporal structures.

That our task may have engaged a distributed timing mechanism related with widespread activity is inferred by our exploratory ROI-based source reconstruction results. Analysis of M1/S1, PMd, SMA, PhG, and DLPFC showed that all brain areas exhibited temporal scaling during preparation and production (Figure 3.7). This indicates a distributed encoding of the necessary temporal information for flexibly switching to the cued sequence speed on a trial basis. The collective cortical engagement may suggest that the temporal processing during planning and execution required activation of core and context-specific areas as part of a large network, in line with a central partially shared timing mechanism model (Merchant, Harrington, et al., 2013). In support of this account, de Lafuente et al. (2022) demonstrated that a distributed network encompassing frontal, parietal, and temporal lobe areas is hierarchically organized in encoding the temporal and spatial features of an event, and a higher-level general sequential state ensuring sequenceness (neural succession) of events. Here the authors proposed that this widespread activity underpins the ability

to estimate and preserve timing in delay periods through internal representations of sensorimotor engrams that are replayed once they have been formed during learning and familiarization with a task. Our present finding of a shared speed modulation mechanism during sequence planning resonates with the engram replay hypothesis in that our participants may have replayed the neural patterns associated with the constituent motor events in the required speed without relying on external sensory cues and/or muscle engagement. The temporal scaling during sequence execution from memory was accompanied by correctly timed motor responses depending on the planned speed, suggesting the maintenance of time representations over sequence completion.

The temporal scaling ability to adapt a movement sequence by changing its speed has been demonstrated behaviorally in humans during sequence execution showing that after extensive training accurate reproduction from memory is achieved at different speeds (Hardy et al., 2018; Slayton et al., 2020). Our design did not allow for investigating a training effect on improved temporal scaling capacity as previously shown in timing paradigms (Keele & Summers, 1976; Slayton et al., 2020; Summers, 1975). However, the scaled EMG movement-related patterns during production (Figure 3.5a, right; *Production*) and the respective behavioral motor press timings (Figure 3.5a, left; insets in *Production*) indicate that our participants received adequate training to successfully adjust the correct tempo during execution.

Although temporal scaling was observed in both preparation and production periods, we found no relationship between the movement-related patterns in the two periods. This uncorrelated scaled timing behavior may indicate that while the brain uses the same temporal modulation strategy, preparatory activity is not identical to movement-related activity (Elsayed et al., 2016). This is in line with findings from the nonhuman primate motor cortex showing that neural population responses operate at orthogonal subspaces during movement preparation and generation: Despite unrelated activity patterns, these neural populations employ computations for withholding preparatory activity to delay movement onset or transferring activity to the movement subspace in the transition to movement initiation (Elsayed et al., 2016; Kaufman et al., 2013, 2014). Our sequence execution scaled results alongside the respective motor press timings corroborate that the required information was passed after the *Go* cue manifested by well-timed sequence generation.

Despite common (within-subject) effector identities for the first press across the two target sequences, we found no evidence for prominent muscular preparation of the first press position as reported previously (Kornysheva et al., 2019) (Figure 3.4b, right). Contrary to the task in the study

of Kornysheva et al. (2019), our task imposed a speedy response of the first press of a sequence as fast as possible after the *Go* cue. This requirement may have engaged inhibitory mechanisms serving the prevention of potentially premature motor responses (Boulinguez et al., 2008; Duque & Ivry, 2009). As such, the observed invariant first press related EMG pattern may be a manifestation of cortico-spinal suppression, at the end of the preparation period, of the forthcoming first press to ensure a timely correct movement upon the signal for sequence initiation (Duque & Ivry, 2009).

Our behavioral results imply a fine-grained modulation of movement availability during planning which distinguishes plan representations depending on movement type, namely on whether a movement belongs to a planned sequence or not. Specifically, we show that while pre-activated sequential movements are facilitated relative to unprepared single ones (Mantziara et al., 2021), they carry an overall sequence cost compared to prepared single movements. The latter point may be readily reflected on the RT initiation results showing a faster initiation for a single movement than a sequence (Figure 3.2c, e, left). This suggests that facilitation in the availability of sequential movements during planning was reduced across a number of movement elements, thus possibly delaying sequence initiation, as opposed to a single movement (Bullock & Rhodes, 2003; Sternberg et al., 1978). Conversely, the limited facilitation of the unprepared single movement reflects its suppression most likely due sequence retrieval. Especially, its slowing (*cf.* RTs) is not comparable with RT costs seen in deviant motor responses performed with the alternate hand (Ostry, 1983; Scaltritti et al., 2018; Shaffer, 1978) as here only the right hand was used for all movement conditions. At the same time, the facilitated (faster and less erroneous), yet graded, planned sequential movements or the even more facilitated prepared single movement cannot be interpreted in the context of a more efficient planning process (Seegelke et al., 2021; Valyear & Frey, 2014, 2015). The latter account proposes that behavioral advantages occur due to repetitive presses with the same effector. However, since in our task *Probe* trials for sequential and control movements were randomized and interspersed with sequence and single press trials, the observed facilitations may be supported by access to separate abstract plan representations of movement types.

Conclusions

Using behavioral probes and decoded EEG cortical activity, we show that serial order of upcoming sequential movements and timing are represented independently during planning of sequences of different speeds. Our work supports the idea that the sensorimotor system and interacting areas employ a mechanism of flexible motor timing which transfers across sequences of different temporal structures. This timing mechanism which appears to flexibly modulate the temporal rehearsal of upcoming movements complements the behavioral CQ readout of serial order which at the same time encodes the preparatory weight of movements depending on their position in the planned sequence. Our findings have important implications for explaining variations or diverging evidence for order and/or timing difficulties in skilled sequencing seen in movement disorders of the cortico-basal ganglia-cerebellar network (Agostino et al., 1992; Altgassen et al., 2007; Avanzino et al., 2013, 2016; Fritsche et al., 2020; Harrington & Haaland, 1991; Jones & Jahanshahi, 2015; Rafal et al., 1987; Reilly & Spencer, 2013; Spencer, 2015). Additionally, clinical populations exhibiting mainly timing deficits in sequence performance may benefit from investigations of a potentially impaired neural mechanism of timing modulation during sequence planning that could be improved through fine-grained passive (Cadena-Valencia et al., 2018), rhythmic (Merchant & Honing, 2014; Thaut, 2013) or neuronal oscillatory entrainment (Amengual et al., 2017; Helfrich et al., 2014).

3.7 Author Contributions

M.M. and K.K. conceived and designed research; M.M. and C.E. performed experiment; M.M. and K.K. analyzed data; M.M. and K.K. interpreted results; M.M. prepared figures; M.M. drafted, edited, and revised this Chapter.

Chapter 4
Discussion

In what follows, I provide an overview of the thesis' empirical findings and underscore the importance of this work. The present findings are then interpreted in relation to the current knowledge in the field. Relevant limitations characterizing this work as well as future directions that emerge from outstanding questions are discussed in an interwoven manner alongside the implications of this research.

4.1 Thesis Overview

There is a clear consensus in the literature that motor planning plays an important role in properties of subsequent production of movements (Al Borno et al., 2020; Haith et al., 2016; Keele, 1968; Klapp, 1976, 1995, 2003; Klapp & Erwin, 1976; Riehle & Requin, 1989; Rosenbaum, 1985, 2010). During task-relevant delays prior to movement sequence initiation, brain activity carries information for predicting not only forthcoming movements (Ariani et al., 2022; Gale et al., 2021) but also the level of sequence performance (Averbeck et al., 2002; Kornysheva et al., 2019). In line with a CQ account, several neurophysiological studies provide support for a parallel preactivation of sequential elements prior to movement initiation competitively queued by their ordinal position (Averbeck et al., 2002; Basu & Murthy, 2020; Bhutani et al., 2017; Kornysheva et al., 2019). Prominent time-based CQ models have proposed that sequence timing is controlled via an integrated timing signal that regulates the ordinal position of each sequential element and makes adjacent elements (e.g., positions 2 and 3 in a sequence) having more similar activations if closer in time than more temporally distant (G. D. A. Brown et al., 2000, 2007; Burgess & Hitch, 1999, 2006; Hartley et al., 2016). In addition, longer time to prepare a sequence has been associated with better preparedness for subsequent execution and accuracy (Ariani & Diedrichsen, 2019). How-

ever, to date the field has lacked a systematic empirical investigation of order and timing representations via a CQ preparatory mechanism and the role of preparation time in organizing preactivated movements before execution.

In Chapter 2, we investigated across three experiments the competitive preactivation of planned movements by probing the behavioral availability of each constituent movement in well-learnt short finger sequences performed from memory and a control movement. In accord with the CQ hypothesis, these experiments revealed the presence of a preactivation gradient as the preparatory CQ mechanism that controls upcoming movements at the end of preparation time to become available for fast and accurate execution depending on ordinal position. An unplanned movement was rather preactivated at a lower level than the sequential movements. In opposition to the prediction of time-based CQ models, sequence timing (temporal grouping and speed) did not regulate movements' preactivation depending on their ordinal position. By contrast, longer preparation times strengthened the preactivation gradient which was associated with improved sequence performance when position-dependent differences were greater. These experiments demonstrate that timing is not part of the CQ mechanism during sequence planning. Instead, more time to prepare a sequence refines the orderly organization of movements to ensure more fluent and accurate performance.

Using the same task, the research presented in Chapter 3 first aimed at reestablishing the behavioral preactivation gradient focusing on speed manipulation (slow *vs* fast) of well-learnt sequences produced from memory. Second, it set out to determine whether at the central neural level (decoded EEG activity) movement-related patterns are preactivated in parallel according to their position in the sequence. In addition, if speed modulation was part of the CQ preparatory mechanism, those patterns would modulate accordingly with movements closer in time (fast sequence) showing similar preactivation levels than movements further apart (slow sequence). This study replicated the behavioral preactivation gradient as well as an absent effect of planned speed on position-dependent differences, in keeping with the findings from the previous experiments (*cf.* Chapter 2). Contrary to the CQ hypothesis, movement-related neural patterns of upcoming movements were not preactivated in parallel. Instead, the EEG decoding results showed a centrally controlled timing mechanism through which movement-related neural patterns were temporally scaled according to the planned sequence speed. These findings indicate that serial order of upcoming

sequential movements and timing are represented independently during sequence planning through different preparatory mechanisms that may complement each other.

The main contributions of this work are multifold. First, it provides a comprehensive experimental basis for unpacking a behavioral and neural code for serial order and timing during the planning of skilled motor sequences. The novel behavioral paradigm employed in this line of research makes this work the first to have behaviorally assessed the preparatory organization of movements prior to sequence initiation. This expands the field's knowledge on the operation of CQ as a preparatory mechanism dedicated to a code for serial position in the context of planning well-practiced motor sequences. It also offers new empirical data to feed the design of augmented LTM CQ models which could form a CQ framework focusing on the mechanics of position-based encoding. Importantly, the modulation of the CQ preparatory mechanism by preparation time advances our understanding of the role of this pre-movement period and its relation to the quality of subsequent sequence performance. An additional novelty of the current work is that, using the EEG modality and signal pattern decoding, it demonstrates that movement sequences can be decoded from preparation to production. Crucially, it reveals for the first time a putative timing preparatory mechanism operating in the human brain which flexibly modulates preactivations of upcoming movements depending on the intended speed. Thus, this research sheds further light on the idea that the core features of sequence organization under investigation - order and timing - may be regulated by different control systems.

4.2 Research Implications

4.2.1 Evidence in favor of a competitive queuing account: Sequential movements are prepared in parallel before execution

Early on, motor science was geared to the idea that movements are prepared before we execute them (Ghez et al., 1991; Henry & Rogers, 1960; Rosenbaum, 1980; Sternberg et al., 1978). In particular, the influential motor programming hypothesis (Keele, 1968; Keele & Summers, 1976; Lashley, 1951) was the first to put forward that motor programs are movement plans that are simultaneously preactivated and contain parameters determining upcoming sequence execution. At the same time, the advancement of CQ neural networks through the years brought out their strong advantage of explaining a variety of cases of human behavioral benchmarks, namely errors

and RTs of sequential elements, by reproducing previous seminal behavioral data (e.g., Baddeley, 1968; Ryan, 1969; Sternberg et al., 1978). Specifically, CQ models have demonstrated via simulations of sequence production data how serial order of elements is associated with these measures, by showing error and RT increases as a function of serial position which, closer to the end of the sequence, level off or even decrease relative to previous positions (Boardman & Bullock, 1992; Farrell & Lewandowsky, 2004; Hurlstone & Hitch, 2015). In contrast to those production-related CQ dynamics, here, we investigated for the first time the parallel preactivation of sequential movements using the above behavioral measures as indirect proxies of movement availability *during planning*.

The acquired RTs and errors to probed positions at the end of a preparation period, revealed a gradient featuring position-dependent differences that reflected a graded movement availability depending on ordinal position. The consistent finding of a preactivation gradient of sequential movements observed across four behavioral test sessions (*cf. experiments 1, 2, 3,* and *4*; Figures 2.2a, b, and 3.2a) suggests that upcoming movements were preactivated in parallel, yet at different levels depending on their position in the sequence. This finding converges with evidence for a neural CQ signal reported elsewhere (Averbeck et al., 2002; Kornysheva et al., 2019), reflecting parallel preactivation of movements organized by ordinal position. Overall, these data cannot be accounted for in a context of a chaining mechanism. If serial order was supported by inter-item associations, the same task would possibly have incurred a facilitated first position and invariant responses of movements associated with the rest probed positions.

The position-dependent preactivation gradient (also referred to here as preparatory CQ gradient), reported here, exhibited some differences between RTs and errors during planning: While errors consistently showed increases with serial position up to the 3rd position, RTs mainly showed position differences up to the 2nd position (except in *experiment 3*). This ostensible discrepancy possibly reflects what these measures represent. In a CQ network, RTs mirror the time that a movement element (the one with the strongest activation) takes to become the winner and exceed the response output threshold through self-excitation and inhibition of neighbors (e.g., see Boardman & Bullock, 1992). In this context, this measure rather reflects a degree of readiness driven by the activation strength and excitation/inhibition dynamics of the candidate movement element which is about to be output. There is a possibility that since our task probed movements just before exe-

cution, movements did not go through the CQ process (self-excitation→inhibition of neighbors→output→self-inhibition/deletion from the planning map). That said, the RTs of 2nd position possibly constitute a readout of a movement struggling to pass through the competition with a still activated 1st position in place since the latter was never in fact executed. Accordingly, the RT attenuation after the 2nd position which levels off with the following positions suggests an accumulative difficulty of these positions to take over as they have to compete more movement plans (1st and 2nd) and their more strongly activated movement plans. This is corroborated by our error pattern results (Figure 2.3) which confirm a persisting tendency of selecting the movement with the strongest activation, that in the 1st position, no matter which other position was probed.

Errors, on the other hand, have been proposed to be linked to a direct readout of activation strength of simultaneously active movement plans in the parallel planning map (*cf*. primacy gradient) as middle movements with weaker activations during planning were found to be more erroneous during execution than earlier or later movements (Averbeck et al., 2002) replicating the inverted U-shaped serial position curve (Deese & Kaufman, 1957; Jahnke, 1965; Murdock, 1962; Robinson & Brown, 1926). This is in agreement with CQ models, predicting that the first and last sequential positions lying at the sequence boundaries show stronger positional representations because they face less competition (Boardman & Bullock, 1992; Farrell & Lewandowsky, 2004; Hurlstone & Hitch, 2015). Therefore, given the nature of the present task, our data point to the error-based preactivation gradient being a more robust readout of movement availability as it likely constitutes a behavioral translation of the preactivation level(s) as formed at the primacy gradient of the CQ system (Grossberg, 1978b, 1978a). However, our experiments did not show a consistently distinct plan representation for the movement associated with the last probed position (4th), as only in *experiments 2* and *4* that movement was less erroneous than the one associated with the 3rd position. This is in line with a neural preparatory CQ gradient showing a high-level positional code that transferred across different sequences, yet the last movement (5th) did not possess a differentiated positional pattern compared to its preceding 4th movement (Kornysheva et al., 2019). Therefore, our finding suggests that the last sequential position might not have exhibited a strong positional representation at the end of sequence planning.

It is important to note that the preparatory CQ gradient possibly reflects a high-level representation of movement sequence organization with regard to encoding and retrieving order, mediated by major memory systems (WM, LTM). Several CQ theorists see this as a potentially 'global'

mechanism that could provide the basis for explaining many types of serial behavior beyond just motor, addressing what Lashley (1951) described as the problem of syntax of action in an attempt to identify its underlying principles. Does that mean, then, that the preparatory CQ gradient is a higher-order, i.e., *cognitive*, readout of a sequence in preparation, suitable for explaining the ability of the brain to represent order (Krakauer et al., 2019; Wong & Krakauer, 2019)? It may be so, as it has been shown to operate at the level of the frontoparietal network detected in the DLPFC (Averbeck et al., 2002). We show, nevertheless, that the position-dependent differences manifested in the error-based preactivation gradient (Figure 2.2c) were explained by very rapid responses to the probed positions (*cf. Probe* trials). That is, not only were participants able to organize the cued sequence in the target order but importantly they produced each response very fast. This suggests that they did not utilize time to deliberate and decide what movement to select. It, instead, shows that the gradient was the readout of an automatic preparatory process which is unlikely to be accounted for by higher-order executive cognitive processing such as action selection and decision making. This may suggest that the CQ mechanism also operates at lower-level motor circuits as shown in the indirect pathway of the BG (Bhutani et al., 2013) and the cerebellum (Kornysheva et al., 2019) before movement execution. In line with this, the RT-based CQ gradient may be the imprint of automatic and necessary RT calculations accounting for motor-related preparation (Haith et al., 2016) of each sequential movement element being, nonetheless, bound to the CQ loop. Additionally, our data advocate that the CQ gradient reflects the preparatory level of constituent sub-movements of a well-learnt finger sequence which had reached the level of a motor skill, since each sequence was smoothly executed with high spatiotemporal accuracy and motor precision (*cf. Sequence* trials). Therefore, these findings corroborate that these skilled sequences were transiently prepared contradicting the position that such motor sequence tasks using discrete sequential movements only address abstract spatiotemporal representations of learned sequences (Krakauer et al., 2019; Wong & Krakauer, 2019).

4.2.2 Competitive queuing as a code for serial order

The preactivation gradient featured differences in movement availability by their serial position that were invariant of the planned sequence timing (Figure 2.2a, b; *experiments 2* and *3*; Figure 3.2a). In rejection of predictions of time-based CQ models, this finding confirms that this mechanism accounts for a preparatory behavioral code for serial order, i.e., ordinal position of

sequential movements, without interacting with sequence timing. It is also of note that the gradient reflected effector-independent position differences, as we obtained similar position-dependent differences despite the use of different finger order sequences across participants. These data resonate with context-based CQ models that employ the position marking and primacy gradient mechanisms for representing order without though incorporating a temporal code, i.e., a timing context signal (Henson, 1998a, 1998b, 1999; Hurlstone & Hitch, 2015, 2018; Lewandowsky & Farrell, 2008). The primacy gradient of simultaneously active plan representations (*cf*. parallel planning layer) is formed by receiving dynamic input from a position marking mechanism (*cf*. positional context layer) responsible for assigning positional representations to sequence item representations (here, movement elements). The positional context layer comprises a signal of sequentially activated nodes representing positional cues or marks. In such CQ systems, it is the positional representations at this higher level of the network architecture that determine which sequence element will be the strongest to be released for execution. This is primarily due to item-position associations emerging during sequence learning; as a result, during sequence retrieval each sequential item becomes most activated (hence, wins the competition after) when the position it was associated with during learning matches the currently activated positional mark. Notably, our data of a dynamic effect of preparation time on the position-dependent gradient illustrate that the gradient expanded with longer preparation times (Figure 2.2a, b; *experiment 1*). This finding points specifically to the potential operation of such a positional context layer which might vary as to how it affects the items' activation within different preparation windows.

In a CQ model for sequence preparation, we propose that associations between plans of sequence element representations in a parallel planning layer and their respective position nodes in a positional context layer are formed during learning (Houghton et al., 2022). The positional context features a positional tuning of the nodes which controls positional differences between plans via a tuning parameter. The accuracy of the tuning parameter may reflect how well a sequence was learnt due to variant training exposure or inter-subject sensorimotor variability. A narrow tuning defines a more accurate sequence plan with distinct positional differences between sequence elements. Thus, it produces a more expanded CQ gradient which becomes more pronounced at later timepoints of sequence preparation. Conversely, a wide tuning introduces noise in item-positional pairing and thus yields a compressed CQ gradient of plan representations which stays relatively the same throughout preparation. Except for positional encoding, this model is also

designed to explain subsequent correct performance based on quality of positional differences during planning on the basis that a more accurate sequence plan (narrow tuning→expanded CQ gradient) is assumed to control a robust orderly organization of movement which facilitates, in turn, fluent sequence initiation and accurate execution. Therefore, it would readily account for our data showing an association between a pronounced preparatory CQ gradient with more fluently initiated and temporally accurate sequences (Figure 2.4).

Contrary to the vast majority of CQ studies which focus on modelling STM for serial order, the above proposed model presumes some kind of intermediate-term memory or LTM sequence representation, albeit not implemented in the network. This thesis presented findings in support of a behavioral CQ code for serial order based on data from LTM which no existing CQ model to date can fully account for. Our participants were trained for two days in producing from memory short unimanual finger sequences with high accuracy. These sequences were of minimal spatial (i.e., finger order) demands per participant (two finger orders in *experiment 1*, one finger order in *experiments 2, 3,* and *4*) and specific temporal structures. Throughout the training stages, although our experiments followed a randomized design for trial presentation, maintenance of serial order during sequence learning was likely mediated by the Hebb repetition effect (Hebb, 1961). This is a consistent effect observed when successive repetitions of the same sequences lead to improvements in ISR of order. Extended to a wide range of memory domains including movement (Kornysheva et al., 2013; Tremblay & Saint-Aubin, 2009), visuo-spatial (Couture & Tremblay, 2006), or visual sequences (Horton et al., 2008), the Hebb repetition effect is thought to be the process through which order of sequential elements is encoded (Hurlstone et al., 2014).

A CQ system adopts the Hebbian mechanism as an exposure process to strengthen positional tuning (i.e., degree of item-position associations) through repetition (e.g., Burgess & Hitch, 1999; Page & Norris, 2009). The CQ modelling of LTM sequence representation involves the incorporation of an interface with WM where the two systems exchange information for correct sequence encoding and generation (Burgess & Hitch, 2005). It has been proposed that Hebb repetition is a good candidate mechanism for supporting this WM -LTM interaction (Burgess & Hitch, 2006). It has also been shown that LTM representation for serial order is possible in an expanded hierarchical model where sequences are 'transferred' from WM to LTM during learning and retrieved from LTM rapidly as chunks back to WM where they are 'decomposed' into their constit-

uent elements (Rhodes & Bullock, 2002). Then, in the WM environment, the positional information defining the order of each element is accessed via the episodic buffer which receives this input from another positional context signal in the LTM environment. Such an operation is possibly applicable to our data by adding to the proposed CQ model for sequence preparation (Houghton et al., 2022) a separate LTM module containing its own positional context which would feed the WM module upon sequence retrieval.

4.2.3 Motor timing during sequence planning: A separate control mechanism?

Collectively, our behavioral (*experiments 1-4*) and EEG results (*experiment 4*) provide evidence that serial order and timing are controlled by separate mechanisms. Our analysis of the normalized decoded EEG signal demonstrates that preparatory neural patterns associated with sequential movements of the cued sequences were scaled over the preparation period according to the corresponding planned speed (Figure 3.5). This scaled serial preactivation suggests that participants covertly rehearsed the timing pattern of the planned sequence during the delay from *Sequence* to *Go* cue.

The observed rehearsal might find its substrate to some kind of intrinsic 'offline' sequential activity (Buhry et al., 2011) consistent with the speed of the cued sequence. Influential research in the rodent brain has shown replay activity originating in the hippocampal place cells[7]: These reactivate memories of past spatial sequences during sharp-wave ripple (SWR) events (Pavlides & Winson, 1989) at a time-compressed manner (~ 20 times the actual/experienced speed) during sleep or rest (Davidson et al., 2009; Karlsson & Frank, 2009; A. K. Lee & Wilson, 2002; Nádasdy et al., 1999). Such reactivations have been reported to occur in both forward and reverse orders before and after active task engagement, respectively (Diba & Buzsáki, 2007). Additional work has shown that hippocampal place cells in the rodent also exhibit slower reactivations, close to the rate of the experienced speed, during sleep (Louie & Wilson, 2001; Ribeiro et al., 2004) or pauses in a spatial alternation task (Denovellis et al., 2021). The latter findings suggest that replay activity encodes variable speeds of experienced sequential events which may facilitate memory storage, updating and retrieval (Denovellis et al., 2021). Interestingly, this dedicated hippocampal replay

[7] Hippocampal place cells encode a subject's position in space, i.e., location in the environment, not ordinal position within a sequence of events *per se*, by increasing their firing rate for certain locations (Dehaene & Brannon, 2011).

of familiar sequences has been reported to co-exist with hippocampal preplay activity, i.e., a differentiated sequential firing pattern that occurs during sleep or rest prior to novel spatial tasks and is thought to encode and facilitate future experiences (Dragoi & Tonegawa, 2011).

Hippocampal replay is thought to play a central role in memory consolidation and planning of goal-directed behavior during spatial navigation (see Ólafsdóttir et al., 2018) and was specifically proposed as a possible mechanism of episodic memory consolidation for preserving temporal order (Diba & Buzsáki, 2007; for a review, see Buzsáki, 2015). As a result of the memory consolidation process, replay events are also detected in cortical circuits showing coordinated reactivation synchronized with the hippocampal SWR during sleep (e.g., Euston et al., 2007; Ji & Wilson, 2007; Rothschild et al., 2017). This coordination reflects the transition of the rigorously retained new memory representations in the hippocampus to the neocortex to support LTM storage and retrieval (Buzsáki, 1996, 2015; Lisman & Morris, 2001).

Indications of non-hippocampal replay are also reported in humans, though in the absence of direct recordings of SWR activity hence constituting indirect evidence (Ólafsdóttir et al., 2018). For example, compressed neural firing rates have been directly observed in the human motor cortex of tetraplegic patients using intracranial multi-unit recordings during rest intervals between periods of performing a motor sequence task (Eichenlaub et al., 2020). In addition, using MVPA classification analysis of BOLD fMRI signal in the visual cortex, Wittkuhn and Schuck (2021) were able to decode the sequential order of five-element visual events presented in different speeds. After sequence presentation, participants had to indicate the position of a previously presented image in the sequence. Event-related patterns showed a rank order probability depending on serial position, over the period between a visual event and a response. Importantly, the slower the sequences the more each event-related pattern probability peaked at timepoints further apart. This indirect evidence of cortical replay events may well reflect coordinated replay activity which is distributed across multiple cortical areas in order to meet the requirements of a current task.

From the above, two important questions inevitably arise: First, since hippocampal-driven replay supports episodic (declarative) memory encoding and consolidation, in what way could this neural phenomenon drive activity underlying a delayed production motor sequence task which might have also involved motor (procedural) memory? Following the long-held dichotomy pertaining to the two memory systems as to both their functional role and their neural substrates, mounting evidence have been pointing to an interactive relationship that supports motor sequence

acquisition and consolidation (Albouy et al., 2008; S. Kim, 2020; Poldrack & Packard, 2003; Rieckmann et al., 2010; Shohamy et al., 2008). These show that across initial learning the hippocampus competes with the striatum, a BG structure subserving procedural memory, which compartmentalizes its contribution depending on the learning stage (Lehéricy et al., 2004, 2005). Thus, it has been proposed that the hippocampus plays a major role in early motor skill learning, mediated by the involvement of the prefrontal cortex for rehearsing temporal order (Ashe et al., 2006), whilst the striatum takes over at later learning stages where motor sequences have become more automatic with practice (Albouy et al., 2013). That said, it is very likely that our task which has involved short-term sequence training (two days) reflects activity associated with intermediate-term memory storage supported by hippocampal (and prefrontal) participation manifested as replay activity.

Subsequently, a second question regards whether hippocampal reactivation events may also a) control action planning and b) encode temporal information, i.e., the timing pattern, of the past experienced sequences. Recent work has challenged the view that replay supports planning of to-be-performed trajectories in spatial navigation tasks (Gillespie et al., 2021). The authors designed a task featuring a multiple-location setting where the rat could explore various spatial trajectories. The findings suggest that replay activity did not reflect the upcoming action (trajectory), but instead replay was associated with locations that were consistently coupled with a reward in the past or locations that were not recent experiences. Regarding the second strand of the question, it should be noted that the earlier mentioned studies reporting putative replay activity in humans (Eichenlaub et al., 2020; Wittkuhn & Schuck, 2021) do not provide strong, direct evidence that replay encodes the temporal segregation of the events comprising the previously learnt or perceived sequence. Instead, their findings most likely indicate a cortical distribution of replay reflecting an intrinsic organization of hippocampal cell population into temporal sequences (Dragoi & Buzsáki, 2006; Friston & Buzsáki, 2016; Harris et al., 2003) as a key mechanism of memory storage during idle states.

In light of the fruitful replay literature and the potential role of hippocampal cells in encoding space and/or time, Buzsáki and Tingley (2018) have argued that the feature of hippocampal activity to occur at different timescales relative to the perceived sequence renders the hippocampal system an inaccurate estimator, even less a predictor, of the real-world spatiotemporal structures. Instead of being a specialized structure in representing those sequence features, data indicate that

it is more likely that the hippocampus and surrounding parahippocampal structures are responsible for 'perceiving', so to speak, a sequential context; by concatenating events and generating neuronal assembly sequences, this system ensures encoding and retrieval of temporally successive events without caring about their temporal structure (Deuker et al., 2016; Garvert et al., 2017; Hsieh et al., 2014; Nielson et al., 2015). In support of this working hypothesis (see also Friston & Buzsáki, 2016), recent multi-unit recordings from the monkey brain show that spatiotemporal events are controlled by a network of areas hierarchically organized as to what extent they encode space (here, right and left positions) and time during a metronome task (de Lafuente et al., 2022). All recorded areas (SMA, prefrontal cortex, lateral and medial parietal lobe, visual cortex, and the hippocampus) showed more or less scaled oscillatory activity which changed depending on the target tempo of the visual metronome. There was, nonetheless, a differentiation regarding the encoding weights for space and time that each area carried. SMA accounted to the greatest extent for the tempo (speed) of the metronome. Spatial information was encoded in the visual cortex, while the lateral intraparietal cortex encoded tempo and space to a similar degree. Interestingly, the hippocampus showed strong encoding for following separate neural trajectories representing the sequentiality of metronome's 'position' (right, left, right, left, and so on) with minimal encoding of either space or tempo.

The above remarks support the idea that the hippocampus is a higher-level controller of spatiotemporal sequences and is rather unlikely that hippocampal reactivations can account for our temporally scaled EEG results during planning. Instead, this finding may reflect the timing readout of cortical firing patterns synchronized with movement event onsets, as shown for example in the SMA (Cadena-Valencia et al., 2018), and detected by striatal neurons which learn with experience to encode temporal durations between events (Allman & Meck, 2012; Matell & Meck, 2000, 2004). This process is part of the engagement of the cortico-thalamo-basal ganglia circuit in interval timing (Coull et al., 2008, 2011) being key in the operation of a central timing mechanism for controlling timed behavior that is shared among multiple areas (Merchant, Harrington, et al., 2013). Specifically, the core timing network (SMA and BG) interacts with other regions such as prefrontal, sensorimotor, auditory, visual cortex, and/or the cerebellum (Figure 2c; Merchant, Harrington, et al., 2013) in order to control motor timing, depending on the task demands and the specific temporal context of movements. In line with this, it is likely that the temporally scaled

rehearsal reported here reflects the participants' ability to have formed dedicated time representations during learning which were deployed during retrieval of a sequence speed condition. Importantly, we show that these representations contained a timing signal on a trial-by-trial basis during sequence planning, which was absent at the muscular level corroborating the deployment of a high-level, centrally controlled signal (Figure 3.5). Additionally, our decoding analysis of a control planned single movement revealed that its timing co-occurred with the first sequence position during planning and execution with this observation being absent at the periphery (Figure 3.6). This indicates the presence of an abstract (effector-blind) representation of timing at the start of sequence preparation and execution. Further research, however, should dissociate timing from a potential abstract positional code by manipulating the timing press of a control single press condition at later timepoints corresponding to those of sequential press positions (2nd, 3rd, and so on). A single press related pattern activation at those individual corresponding timings would favor a timing rehearsal and reproduction account. Alternatively, we would still see a co-occurrence with the first press position suggesting an abstract code for first position even in the absence of subsequent movement-related patterns as in the case of a single press movement.

Our finding of a high-level timing signal during sequence planning advances the literature in regard to the workings of a timing system that is independent from the control of serial order. The differentiated planning of motor sequences with varying complexity of order and timing has been captured with RPs, with sequences consisting of a complex timing structure and easy order starting to prepare earlier compared to sequences with a reverse spatiotemporal profile (Bortoletto et al., 2011). Previous MEG work has investigated how anticipation of order and timing during incidental, implicit acquisition of complex spatiotemporal finger sequences is associated with oscillatory dynamics in the sensorimotor cortices that might improve sequence performance (Heideman et al., 2018). This study found stronger beta power decreases in anticipation of short temporal intervals compared to long ones with contralateral suppression mediating performance through faster responses. These oscillatory modulations were specific to the temporal structure and were transferred across different spatial sequences. Using MEG decoding, Kornysheva et al. (2019) found a CQ parallel preactivation of upcoming movements ranked by their position in the sequence and that this signal was preserved across sequences of different finger orders and/or timings. However, the above studies did not isolate the spatial and temporal effects on the underlying neural modulations. Specifically, the study of Kornysheva et al. (2019) did not disambiguate

whether the preparatory CQ signal encoded the ordinal position or the temporal intervals of the planned sequence. The authors speculated that the signal might be driven by overlapping positional and temporal representations in a high-level context layer in the CQ model (Burgess & Hitch, 1999, 2006). Here, we extend previous findings by detecting at the behavioral level a mechanism that controls ordinal position without integrating timing (*cf.* CQ preactivation gradient) and a timing rehearsal signal present at the central neural level. This suggests that order and timing are represented independently and the CQ gradient was in effect during sequence planning but not contained in the EEG signal. It should be noted that the task in the previous study (Kornysheva et al., 2019) was based on a two-by-two design where participants had to learn and produce from memory four different combinations of spatiotemporal sequences thus increasing the demand of reorganizing the ordinal position. The present task, on the other hand, required a focus on changing the speed while retaining order, thus most likely tapping on the aspect of interval timing encoding and retrieval. Alternatively, the difference in findings might be explained by the EEG sensitivity to detect both radially and tangentially oriented current dipoles, whilst the former are not recorded by MEG hence producing no signal (Ahlfors et al., 2010; Cohen & Halgren, 2003; Singh, 2014). This explains the capacity of EEG to record a richer map of cortical neuronal assemblies that might have sent considerable input to the core timing network presumably engaged in this task, as discussed previously. Moreover, our exploratory analysis of the decoded EEG signal at the source level in five critical regions implicated in planning or execution (M1/S1, PMd, SMA, PhG, DLPFC) showing timing rehearsal most strongly during sequence planning (Figure 3.7) cannot preclude that a CQ parallel positional code can be detected at the EEG level. Thus, a future study combining simultaneous EEG and MEG recordings utilizing various sequence conditions would be necessary for addressing whether the CQ operation would still be present in both the MEG and the EEG signals. The co-existence of a positional and timing code at the central neural level would provide input for the architecture of modular CQ or hierarchy-based RNN models where timing is learnt and reproduced by the system as an independent module (Calderon et al., 2021; Zeid & Bullock, 2019).

4.2.4 Quality of the preparatory competitive queuing gradient reflects the motor sequence plan and correlates with performance

At the behavioral level, we also show that the position-dependent preactivation gradient was modulated by the time to prepare a sequence, not its planned timing (Figure 2.2a, b). Previous studies have reported a functional link between planning and performance through correlations between neural representations of movements during planning and performance accuracy (regarding finger and temporal accuracy) during execution (Averbeck et al., 2002; Kornysheva et al., 2019). Additionally, longer preparation times are suggested to result in faster and more accurate (regarding finger accuracy: order, digit identity etc.) execution of temporally unstructured finger sequences (i.e., instructed to be executed as fast as possible), especially affecting the first few movements (Ariani & Diedrichsen, 2019). Collectively, these findings led us to hypothesize that preparation time may play a role in forming a sequence plan representation that facilitates subsequent execution. An alternative hypothesis was that if timing affected the position differences based on how close or far apart in time the associated movements were in the sequence (Burgess & Hitch, 1999; Hartley et al., 2016), it would be the driving force for controlling an accurate sequence plan representation within the CQ gradient. In rejection of the latter hypothesis, we found that the error-based CQ gradient gradually expanded over preparation windows of 500 ms, 1000 ms, and 1500 ms. This suggests that preparation time provides the means for the preparatory CQ gradient to refine the sequence plan by amplifying the relative availability of movements, i.e., increasing their position-dependent differences. Technically, this translates to movements associated with later positions being less available with more preparation time, and conversely, movements associated with earlier positions being more facilitated. Although counterintuitive, such modulation implies that preactivation levels depending on ordinal position became more enhanced ensuring that competition, hence correct output in execution, was not compromised. The scaling of the gradient may be supported by sustained neural activity in the prefrontal cortex explained by sequence retrieval from intermediate-term memory or LTM and maintenance to WM until the *Go / Probe* cue. This prefrontal activity is maintained for variant delay periods (Funahashi et al., 1989; Fuster & Alexander, 1971; Kubota & Niki, 1971) and is thought to reflect the active state of the neuronal population which processes the current information (Lundqvist et al., 2018). Prefrontal sustained activity has been shown to be associated with the strength of the memory representation

for as long it needs to be held in WM until response output, with longer delay periods predicting more accurate responses (Curtis et al., 2004; Funahashi et al., 1989).

Critically, across *experiments 1, 2* and *3* we demonstrate that the position-dependent preactivation gradient, formed in a 1.5 s preparation period, is a preparatory mechanism accounting for improvements in subsequent sequence performance. This was evident when participants with a more expanded gradient (i.e., larger differences between adjacent positions) were able to initiate the planned sequence faster and execute it more accurately as to its temporal structure than participants with a more 'compressed' gradient (Figure 2.4). This is in line with previous findings from Kornysheva et al. (2019) where, accordingly, a more expanded preparatory CQ gradient characterized by well-separated press-related neural patterns predicted temporal and finger accuracy improvements during sequence performance. The inter-subject variability in the preparatory CQ gradient may be explained by individual differences in motor sequence learning. As previously mentioned, a more pronounced CQ gradient may be accounted for by the establishment of stronger associations between each sequential movement and its position during learning. It is plausible that those participants developed such strong positional tuning assumed to enhance movements' differential preactivation hence yielding faster sequence initiation and increased temporal accuracy. Additionally, recent work has shown that practicing motor sequences over several days (five) expands the planning horizon by increasing slightly the number of planned movements, while the planning of the remaining few movements occurs 'online', i.e., during execution (Ariani et al., 2021). Within each day, this increase also correlated with faster and more accurate sequence execution.

In our view, the above two accounts for explaining the association between a pronounced CQ gradient and improved performance observed in our data are not mutually exclusive. Although all our participants received the same amount of training, inter-subject variability in sequence learning and planning capacity may account for differences in the quality of the preparatory CQ gradient (pronounced *vs* weak). It is possible that participants who became more efficient during learning in planning the required movements ahead (i.e., before the *Go* cue) exhibited a more pronounced CQ gradient. Thus, an increased planning horizon may have provided adequate capacity during the preparation period for facilitating stronger positional tuning. By contrast, individuals with a narrower CQ gradient made more temporal errors and delayed sequence initiation. Accord-

ingly, this might suggest that those participants possessed a poorer planning horizon during learning which compromised their capacity to establish strong associations between movement plan representations and their serial position in the first place. A future study using a longer training protocol would possibly address an effect on the quality of the CQ gradient reflecting stronger position-dependent preactivations of sequences following more extensive practice.

The above points regarding the role of preparation time in refining the motor sequence plan and the origins of the quality of the preparatory CQ gradient raise the following questions: How much preparation time is it required for an optimally refined sequence plan or differently put, how much more would the CQ gradient expand past the 1.5 s preparation period? Second, how would the CQ gradient develop when planning longer sequences (> 4 elements)?

Future research should test whether there is a cap in the CQ gradient optimization by thorough examination of the gradient's expansion over incremental 500 – 1000 ms preparation windows beyond the maximum preparation duration used here (1.5 s) or 1.8-2.2 s reported elsewhere (Kornysheva et al., 2019). At least for single reaching movements, it has been proposed that there is an optimal planning time within which a motor response reaches a minimum RT indicating an adequate movement preparation state (Dahan et al., 2019; Haith et al., 2016). Increasing this planning time past this point was found to increase RT (Dahan et al., 2019). Additionally, Ariani & Diedrichsen (2019) suggest that there is a maximum planning time within which only a proportion of a movement sequence can be prepared: Here, five-element finger sequences, trained to be produced as fast and as accurately as possible, benefited from a 1.6 s preparation time during which an average of three movements were prepared. More preparation time (2.4 s) was not utilized for accommodating the rest of the movements which were thought to be subsequently planned 'online' (see also Ariani et al., 2021). Similarly, we report that the preparatory CQ gradient lacked a consistent difference of the last position (4th) compared to the previous position. This may indicate weak positional tuning of the last movement at the end of a 1.5 s planning period, possibly planned subsequently online after the *Go* cue. Based on these findings, we assume that additional planning time in our task would most likely not strengthen the CQ gradient. However, the gradient might be maintained for longer planning periods due to prefrontal sustained neural activity which scales with the delay length before the response is prompted supporting the memory representation of the cued sequence (Curtis et al., 2004; Ikkai & Curtis, 2011; Riley & Constantinidis, 2016).

Last, a future experiment should address the outstanding question regarding the consistency of the preparatory CQ gradient when planning longer movement sequences. To our knowledge, CQ models have simulated sequence recall data from STM for sequences consisted of up to nine elements. A common observation across their findings is that the longer a sequence is, the more errors and RTs increase at the middle serial positions, peaking though at a later serial position as a function of sequence length (Farrell & Lewandowsky, 2004; Hartley et al., 2016; Hurlstone & Hitch, 2015; Lewandowsky & Farrell, 2008). Therefore, we would expect that the preparatory CQ gradient when planning, for instance, a finger sequence of seven elements even from intermediate-term memory or LTM, would show similar RT and error patterns to those reported here. Specifically, movement availability would consistently decrease up to roughly the fifth position because of weak positional representations of the later movements as we have shown here (see also Kornysheva et al., 2019).

4.2.5 Differentiated facilitation of planned and unplanned single movement plan representations relative to sequential movements

Although the focus of this research was on skilled motor sequence planning, we wished to investigate single movements under different conditions as to how these perform relative to constituent movements of a sequence during planning. Movements that occupy a position in a sequence were shown to be preactivated in a competitive manner depending on their serial position as initially learned. By contrast, single movements associated with an unrelated effector, never learnt as part of a sequence, behave differently before execution depending on whether they were planned or unplanned. Specifically, when a sequence was cued but, instead of a sequence position, an unrelated effector was probed, this unexpected, unprepared movement was slower and more erroneous than the last probed sequence position suggesting limited preactivation (Figure 2.2a; *experiment 3*; Figure 3.2a). When, on the other hand, a single press of a prepared unrelated effector was cued, the associated response exhibited increased preactivation compared to the first sequential movement indicating a cost for accessing a whole sequence (Figure 3.2a). In short, although sequential sub-actions were more facilitated compared to an unprepared action, they carried a sequence cost compared to a prepared action, on the grounds that facilitation must be distributed across more actions. The lower preactivation of an unprepared action most likely reflects its relative suppression because both centrally and peripherally the system was prepared for executing a

certain (cued) sequence. On the other hand, a valid account for a more facilitated single movement *vs* a sequence is found in a CQ principle which follows that plan representations comprising the primacy gradient, at the parallel planning layer in the network, are partially normalized (Averbeck et al., 2002; Grossberg, 1978a). That is, total distributed neural activation across plans is reduced as a function of their number which results from how the RCF at the lower, competitive choice, layer controls the recurrent self-excitation of the most active plan and the inhibition of all competitors. The RCF normalization also affects the speed for movement initiation which has been shown to directly depend on the number of active plans in the parallel planning layer: The more plans the slower the RT of the first movement (Bullock & Rhodes, 2003; Sternberg et al., 1978), converging with our sequence and single press initiation RT results.

However, what remains to be resolved is whether the single movement was more facilitated because it was just single (i.e., not sequential) or because it was prepared and delivered with an effector that never belonged to a trained sequence. Previous imaging work has shown distinct sequence-specific neuronal patterns for multi-finger finger sequences (i.e., neuronal tuning sensitive to the sequential context) in premotor and parietal areas, and the SMA (Grafton et al., 1998; Kornysheva & Diedrichsen, 2014; Wiestler et al., 2014; Wiestler & Diedrichsen, 2013; Yokoi et al., 2018) which become pronounced as a result of skill learning (Wiestler & Diedrichsen, 2013). Importantly, during sequence retrieval, encoding of a sequence at an abstract level (i.e., effector-independent) is associated with increases in the inferior parietal cortex whilst the sensorimotor cortex encodes effector-specific information (Grafton et al., 1998). On the other hand, single-finger presses elicit activation in the hand area of M1 and the somatosensory cortex (Yokoi et al., 2018). Thus, the distinct facilitation of a planned single movement and a sequence, observed here, may suggest that participants were able to flexibly access on a trial-by-trial basis the respective plan representations which were characterized by differentiated preactivation level and supported by distinguishable effector-specific neuronal activation. Further behavioral and imaging research, nevertheless, should examine the possibility of a persisting facilitated preactivation of single *vs* sequential movements in the presence of common effectors. For example, if planning a sequence consisting of a middle-little-index-ring or ring-little-index- middle finger order *vs* planning a single press of the ring, still elicits a more facilitated availability of the single press, it would provide stronger evidence for a sequence-related preactivation cost relative to a single movement preactivation. That is, despite that the latter movement condition would be delivered with an effector

included in a trained sequence at different serial positions (first or last), distinct retrieval and differentiated planned availability would still be corroborated by dedicated neuronal activations.

4.2.7 Relevance to brain-computer interface research

Our approach on decoding sequential movements from non-invasive EEG preparatory signals can be considered as complementary to brain-computer interface (BCI) related studies. The development of BCI systems for motor control of assistive devices was originally based on the idea that brain signals of amputee patients contain motor representations that can be detected with neural recording methods (Nirenberg et al., 1971). BCI technologies and related work focus on achieving efficient communication between brain activity and external machines. The goal is twofold (Lebedev & Nicolelis, 2017): One application is the direct generation and control of response outputs so that the human patient end user interacts with the environment through a device, such as a robotic neuroprosthetic effector, which has been designed to decode commands (e.g., Huang et al., 2009; Yang & Leung, 2013). A second application aims at neurorehabilitation via feedback to the patient for invoking plastic changes or entrainment (e.g., Sitaram et al., 2017).

Invasive techniques for brain activity recording, such as Electrocorticography, single- and multi-unit activity, have been successfully used for decoding movement parameters because of their high spatiotemporal resolution (Hauschild et al., 2012; Hochberg et al., 2006; S. P. Kim et al., 2008; Moran & Schwartz, 1999; Mulliken et al., 2008; Slutzky & Flint, 2017). However, non-invasive modalities such as EEG, fMRI, and MEG, have gained ground due to their low risk compared to invasive methods. Since its early use in BCI protocols (Nirenberg et al., 1971; Vidal, 1973), EEG in particular has been widely used in this domain because of its capacity to directly measure cortical activity and its lower cost (for a review and discussion, see Abiri et al., 2019; Saha et al., 2021).

In general, the fruitful BCI-related work using EEG is focused on decoding either effector movements (Liao et al., 2014; Paek et al., 2014; Yoshimura et al., 2017) or movement preparation (Ieracitano et al., 2021), intention (Bulea et al., 2014; Valenti et al., 2021; Yang et al., 2015), or imagery (Ang & Guan, 2017; Cho et al., 2017; Gaur et al., 2021; Kevric & Subasi, 2017; Tabar & Halici, 2017) for contributing to the development of neuroprosthetic technology. In most cases, decoding task aspects from the EEG signal recorded during motor paradigms involves the development, optimization and validation of classification algorithms to improve the decoding accuracy

(i.e., decrease the difference between measured and predicted task aspect). Linear decoders have been used to decode single-finger and repetitive finger movements from the EEG signal during execution (Paek et al., 2014; Yoshimura et al., 2017). Similarly, Yang et al. (2015) developed a linear classifier to decode kinematic parameters (peak speed and acceleration) of center-out reaching movements using EEG oscillatory activity in alpha and beta bands utilizing though the signal from a short preparation period. The authors found that movement parameters were successfully decoded from the planning period alone, but the EEG oscillatory signal from both planning and execution was a better predictor of peak speed and acceleration. Applying deep learning, another group decoded the time frame of movement intention (interchangeably also termed here preparation) before an open or close action *vs* rest based on a 'hybrid' EEG signal from both the time and the time-frequency domains (Ieracitano et al., 2021).

To our knowledge, BCI-oriented literature has not yet explored advanced models optimized for decoding planned motor sequences. In the present EEG study (*cf.* Chapter 3), we trained a Gaussian-linear classifier in discriminating neural patterns of sequential movements from a preparation period based on the signal associated with the sequential motor presses enacted during the production period. By using a trial-fold cross-validation approach (Kohavi, 1995; Lemm et al., 2011), which increases the model's ability to learn the input features (here, neural patterns of the EEG voltage signal) and hence improves its classification accuracy, we showed that the EEG preparatory signal encodes activity associated with to-be-performed sequential movements (Figures 3.4a and 3.5a, left). Importantly, the decoded muscular signal acquired with concurrent EMG recordings (Figure 3.4a, right) can readily act as an additional validation of the model's performance to successfully classify the press conditions: The press-related peak pattern probabilities during the production period coincided with the executed sequential motor presses depending on sequence speed condition (Figure 3.4a, right; color-coded vertical lines of press timings; Figure 3.5a, right), whilst the preparatory press-related pattern probabilities did not vary, in line with an absence of overt movement. Therefore, our findings demonstrate the feasibility of successfully decoding planned motor sequences from non-invasive EEG and can contribute to BCI protocols utilizing the preparatory signal.

4.2.6 Implications for skilled motor sequencing in movement disorders

Serial order and/or timing are compromised in several movement disorders of the cortico-basal ganglia-cerebellar network (Agostino et al., 1992; Altgassen et al., 2007; Bares et al., 2007; S. Brown et al., 2005; Duffy, 2006; Frick & James, 1965; Fritsche et al., 2020; Ham, 1999; Harrington & Haaland, 1991; Malcolm R., 2011; Tükel et al., 2015; Ye et al., 2021). The degree to which these deficits are observed may vary largely depending on disease stage and severity, as well as the medication status and related implications due to 'side' effects and inter-individual variability (e.g., see Ruitenberg et al., 2015). In addition, depending on the clinical population under investigation, studies use different tasks to infer conclusions about order and timing impairment. Such an example is the study of skilled sequencing in Parkinson's disease and BG patients, employing from simple RT (e.g., Rafal et al., 1987), to serial reaction time (e.g., S. W. Kelly et al., 2004; Seidler et al., 2007; Siegert et al., 2006; Werheid et al., 2003) and synchronization-continuation tasks (e.g., Harrington et al., 1998; Spencer & Ivry, 2005). Altogether, this literature agrees on a slower sequence initiation of multi-element sequences but also provides diverging evidence with studies showing or assuming impaired or preserved encoding (see Ruitenberg et al., 2015) and pre-programming of serial order (e.g., Harrington & Haaland, 1991; Reilly & Spencer, 2013; Ye et al., 2021) and variable or intact control of timing relative to the target timing during sequence execution (see Jones & Jahanshahi, 2015). Our present findings can contribute to understanding how sequence planning dynamics can explain these variations and impairments and provide the basis for the design of intervention protocols. Such patients would benefit from neurorehabilitation programs aiming at assessing and modulating movement preactivations and timing. Specifically, our finding of a CQ readout for serial order provides an advantage for assessing behaviorally how the preparatory organization of sequential movements can account for sequence initiation, positional representation, and temporal accuracy variations during execution. In addition, a potentially dysfunctional timing rehearsal signal may be manipulated through neuromodulation, stimulation and neurofeedback (e.g., Bichsel et al., 2021) during sequence planning, such as via regulating gamma bursts to match the target temporal intervals (Cadena-Valencia et al., 2018).

4.3 Concluding Remarks

Serial order and timing of well-learnt movement sequences are integral features of sequence learning, planning and control, usually treated as being two faces of the same coin, i.e., integrated in a common control system. Using a novel behavioral paradigm, this work demonstrates a preparatory CQ mechanism prior to sequence execution which controls the serial order, but not the timing, of simultaneously prepared movements depending on their initial position in the sequence. At the neural level, a separate putative timing engram was present featuring serial preactivations that followed the planned sequence timescale. These findings indicate that the sensorimotor system makes use of hierarchical representations of order and timing during sequence planning. These seem to be driven by different preparatory control systems which ensure that well-timed behavior transfers across sequences of different speeds preserving the correct order of sequential movements. This research advances our understanding of a potential spatiotemporal modularity of motor sequence organization. Further research should shed light on how these modules work together during planning and execution. The present findings have implications for movement disorders which show order and timing deficiencies in retrieving order and processing timing during motor sequence planning.

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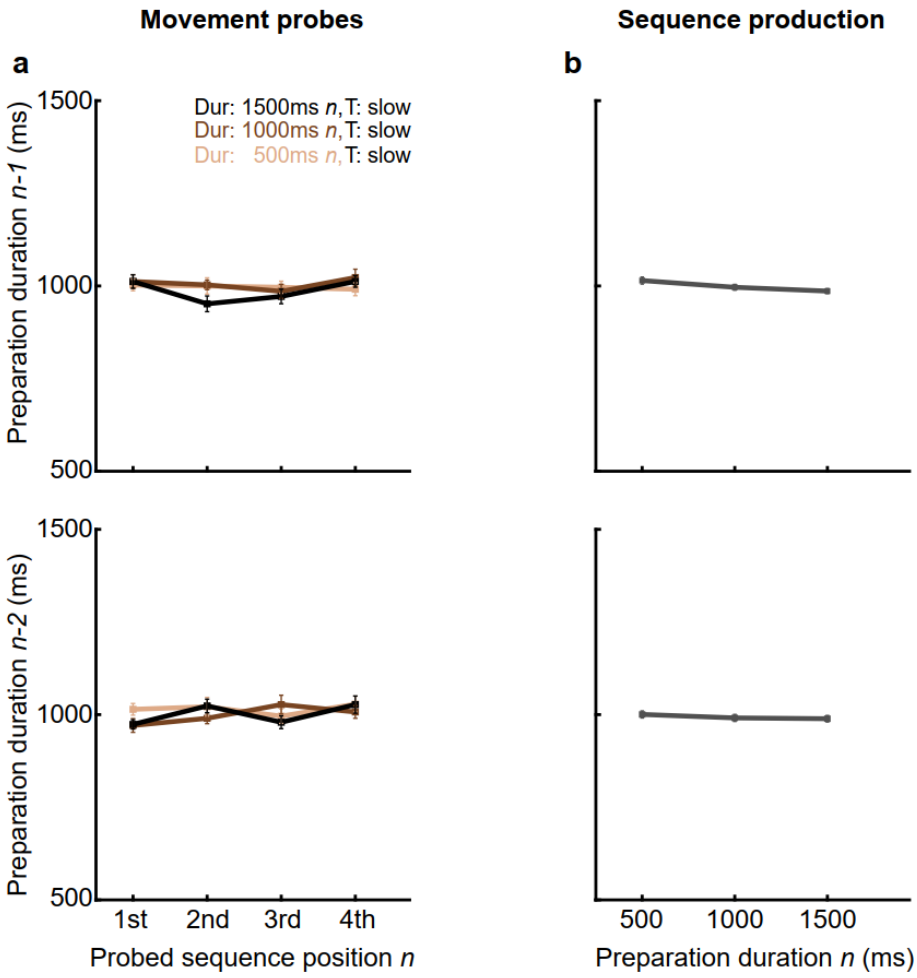
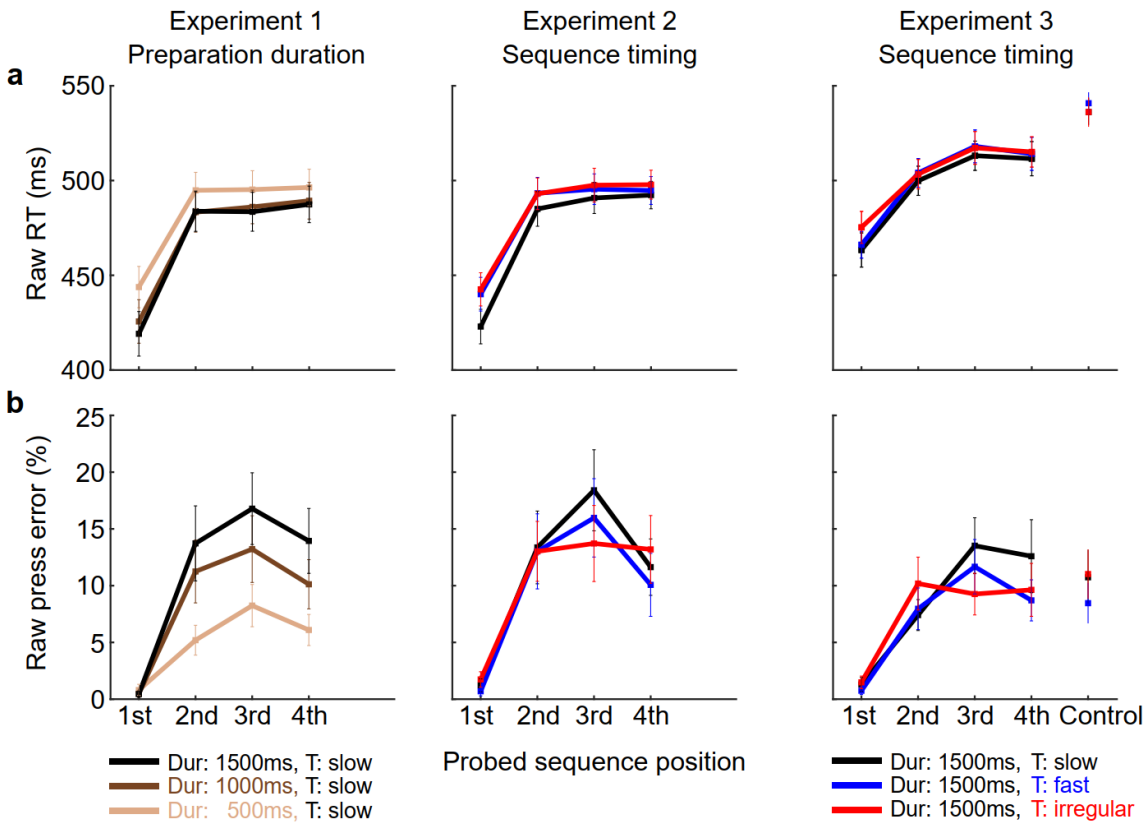
Appendix A

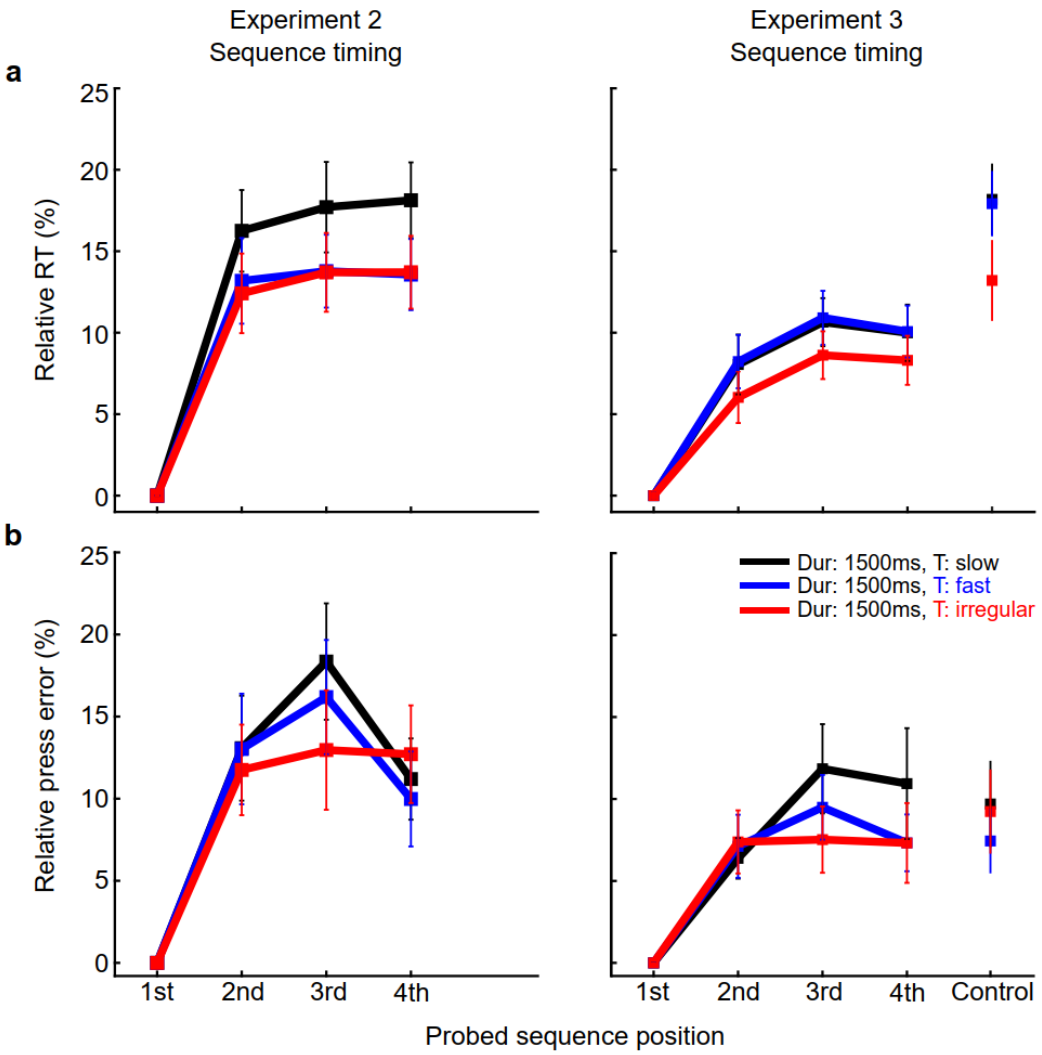
Chapter 2 – Supplemental material



Supplemental Figure A.S1 | Preparation duration in preceding trials in relation to conditions in the current trial in Experiment 1. a. *Probe* trials: Mean preparation duration in preceding trials, *n-1* and *n-2* (first and second rows, respectively), as a function of probed positions in the preparation duration conditions in a current trial (*n*) (4 x 3 repeated measures ANOVAs: Position x Preparation duration *n-1*, $F(6, 108) = .88$, $p = .511$, $\eta^2p = .05$; Position x Preparation duration *n-2*, $F(6, 108) = 1.14$, $p = .344$, $\eta^2p = .06$). **b.** Memory-guided *Sequence* trials: Mean preparation duration in preceding trials, *n-1* and *n-2* (first and second rows, respectively), as a function of the preparation duration conditions in a current trial (*n*) (one-way repeated measures ANOVAs: Preparation duration *n-1*, $F(2, 36) = 2.53$, $p = .093$, $\eta^2p = .12$; Preparation duration *n-2*, $F(2, 36) = .36$, $p = .701$, $\eta^2p = .02$). Error bars represent standard errors.

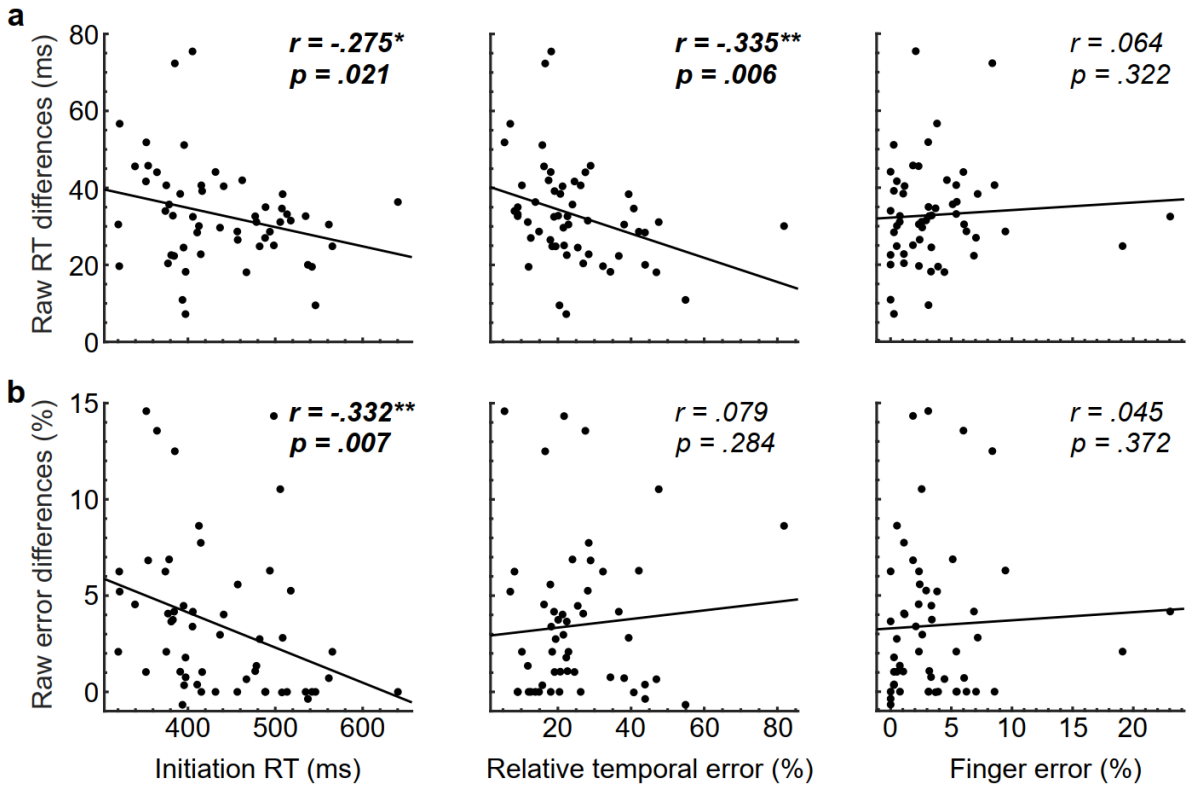


Supplemental Figure A.S2 | Position-dependent movement availability during sequence planning (raw RT and error rate values). Complementary graphs to Figure 2.2, illustrating the raw RT (**a**) and percent press errors (**b**) of probed movements associated with the 1st - 4th press positions of the planned sequence. Error bars represent standard errors.

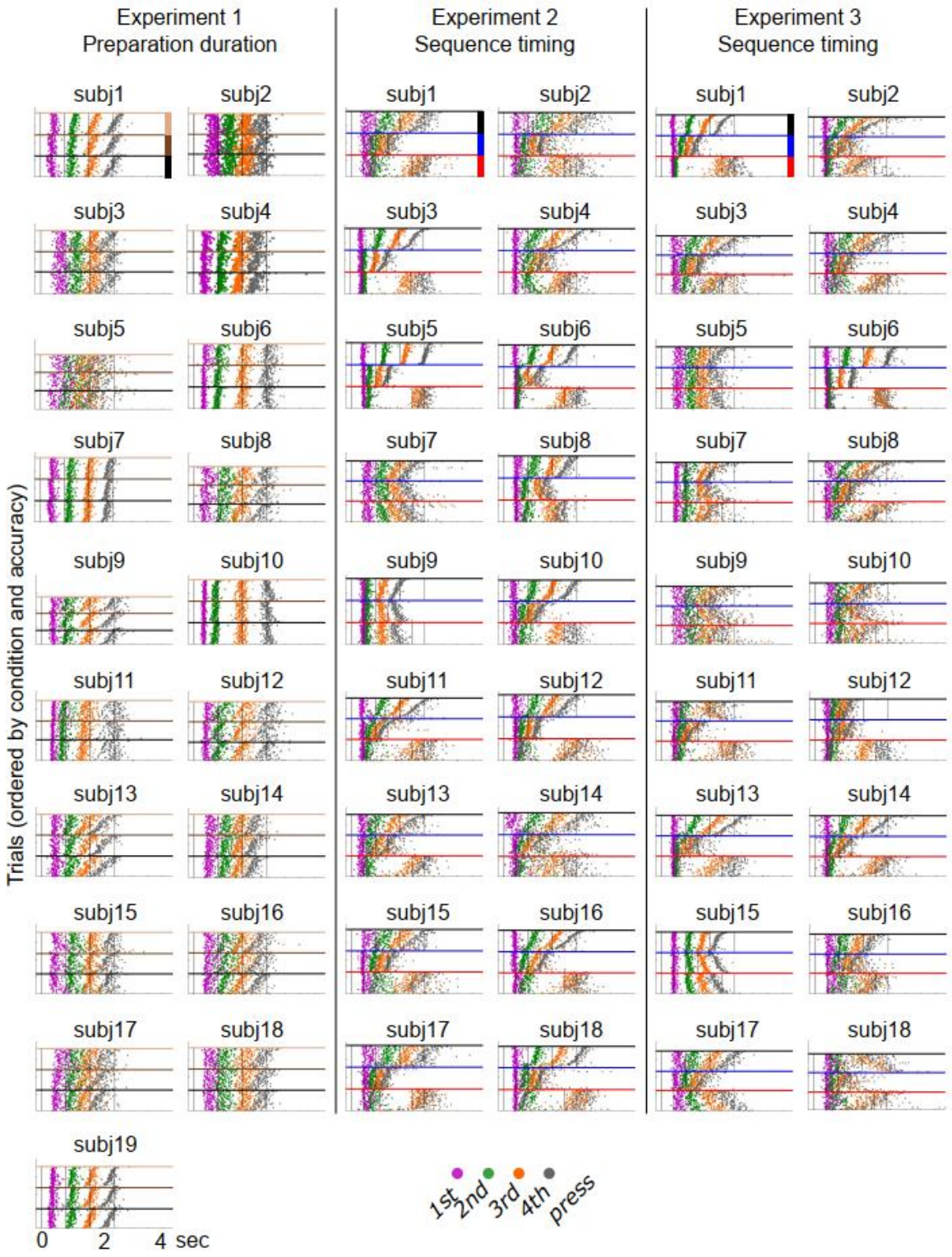


Supplemental Figure A.S3 | Position-dependent movement availability during sequence planning without outliers in relative temporal error. a. In Experiment 2, RT increased significantly from 1st to 2nd position ($t(16) = -7.108$, $p < .001$, $d = 1.72$) whilst 3rd and 4th positions did not change significantly compared to 2nd and 3rd positions, respectively (2nd to 3rd position, $t(16) = -.570$, $p = .289$, $d = .16$; 3rd to 4th position, $t(16) = -.322$, $p = .376$, $d = .07$). Experiment 3 revealed significant RT increases from 1st to 2nd position ($t(16) = -4.264$, $p < .001$, $d = .97$) and from 2nd to 3rd position ($t(16) = -2.155$, $p = .02$, $d = .37$). No significant change was found from 3rd to 4th position ($t(16) = .393$, $p = .35$, $d = .08$). The control movement showed a significant RT increase compared to the 4th position ($t(16) = 3.120$, $p = .007$, $d = .89$). Position did not interact with Timing in either experiment for RTs (Experiment 2, $F(3.264, 52.231) = 2.570$, $p = .059$, $\eta^2p = .138$, Greenhouse-Geisser corrected, $\chi^2(20) = 39.305$, $p = .007$; Experiment 3, $F(3.797, 60.758) = .852$, $p = .493$, $\eta^2p = .051$, Greenhouse-Geisser corrected, $\chi^2(20) = 34.635$, $p = .025$). **b.** Experiment 2 showed significantly increasing errors up to the 3rd position with 2nd and 3rd positions exhibiting more errors than the 1st ($t(16) = -5.816$, $p < .001$, $d = 1.71$) and 2nd ($t(16) = -1.830$, $p = .043$, $d = .41$) positions, respectively. The 3rd position was significantly different than the 4th position ($t(16) = 2.367$, $p = .016$, $d = .54$). In Experiment 3, errors increased significantly from 1st to 2nd position ($t(16) = -7.352$, $p < .001$, $d = 1.80$) whilst there was a marginally significant increase from 2nd to 3rd position ($t(16) = -1.592$, $p = .066$, $d = .50$). There was no significant difference between the 3rd and 4th positions ($t(16) = .766$, $p = .228$, $d = .21$). The control movement did not show a significant increase in errors compared to the 4th position ($t(16) = -.662$, $p = .517$, $d = .22$). Similar to the RTs, Position did not interact with Timing in either

experiment for errors (Experiment 2, $F(6, 96) = 1.696$, $p = .130$, $\eta^2p = .096$; Experiment 3, $F(6, 96) = .696$, $p = .654$, $\eta^2p = .042$). Error bars represent standard errors.

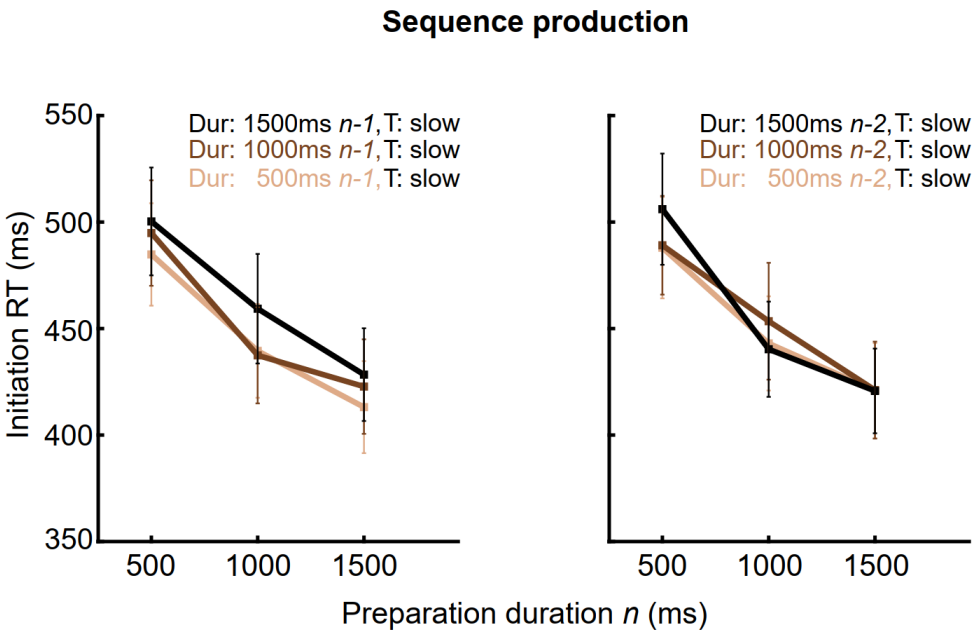


Supplemental Figure A.S4 | Correlation of performance with position-dependent differences in movement availability during planning (raw RT and error rate values). Raw reaction time (RT) in ms and percent press error during preparation (*Probe* trials) were used to calculate the mean difference between adjacent positions (1st - 2nd and so on), reflecting the preactivation gradient size of constituent movements of the planned sequence. **a.** Larger raw RT differences correlated with faster sequence initiation and less relative temporal errors during production. **b.** A negative correlation was similarly found between raw error differences and sequence initiation RT, but not relative temporal error. Neither measure was associated with decreased finger errors (**a, b**; Finger error (%)). All correlations are one-tailed.



Supplemental Figure A.S5 | Finger press timing during sequence production per trial. Individual participants' raster plots show the timing of single button presses for each correct *Sequence* trial produced from memory after the *Go* cue (t = 0) following training (target timing superimposed, gray lines). The colour code of the button presses corresponds to the press position in Figures 2.1 (b, c) and 2.3. Within each condition, trials are ordered from most

accurate to least accurate by the mean deviation from the target interval structure across each trial (colour coding for conditions, *cf*. side bars in first participants panels, respectively).



Supplemental Figure A.S6 | Sequential preparation duration effects in Experiment 1. Memory-guided *Sequence* trials: Sequence initiation RT (*Go* cue to first press) in the preparation duration conditions in a current trial (*n*), split by the same conditions in preceding trials, *n-1* and *n-2* (3 x 3 repeated measures ANOVAs: Preparation duration *n-1* x Preparation duration *n*, $F(4, 72) = .69$, $p = .599$, $\eta^2p = .04$; Preparation duration *n-2* x Preparation duration *n*, $F(4, 72) = 1.77$, $p = .143$, $\eta^2p = .09$). Error bars represent standard errors.

Supplemental Table A.S1a | Position-dependent increases (paired samples t-tests) based on reaction time (RT) and press error (across all RT responses and in fast and slow RT responses).

	Experiment 1								Experiment 2								Experiment 3							
	Reaction time (ms)				Press error (%)				Reaction time (ms)				Press error (%)				Reaction time (ms)				Press error (%)			
Comparison	*df*	*t*	*p*	*d*	*df*	*t*	*p*	*d*	*df*	*t*	*p*	*d*	*df*	*t*	*p*	*d*	*df*	*t*	*p*	*d*	*df*	*t*	*p*	*d*
1st - 2nd	18	-7.449	< **0.001*****	1.32	18	-6.646	< **0.001*****	1.83	17	-6.452	< **0.001*****	1.60	17	-5.512	< **0.001*****	1.57	17	-4.608	< **0.001*****	1.03	17	-7.764	< **0.001*****	1.83
2nd - 3rd	18	0.054	0.479	0.01	18	-1.928	**0.035***	0.27	17	-0.634	0.267	0.16	17	-2.045	**0.029***	0.43	17	2.405	**0.014***	0.40	17	1.884	**0.039***	0.58
3rd - 4th	18	-0.720	0.241	0.09	18	-1.238	0.116	0.21	17	-0.249	0.404	0.05	17	2.604	**0.010****	0.54	17	-0.214	0.417	0.04	17	0.767	0.227	0.20
Control - 4th	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	17	3.044	**0.007****	0.86	17	-0.809	0.430	0.26
	Press error (%)								Press error (%)								Press error (%)							
	Lower RT quartile (fast responses)				Upper RT quartile (slow responses)				Lower RT quartile (fast responses)				Upper RT quartile (slow responses)				Lower RT quartile (fast responses)				Upper RT quartile (slow responses)			
	df	*t*	*p*	*d*	*df*	*t*	*p*	*d*	*df*	*t*	*p*	*d*	*df*	*t*	*p*	*d*	*df*	*t*	*p*	*d*	*df*	*t*	*p*	*d*
1st - 2nd	18	-6.537	< **0.001*****	0.54	18	0.593	0.281	0.20	17	-6.989	< **0.001*****	1.57	17	-0.566	0.290	0.20	17	-6.592	< **0.001*****	2.12	17	-0.343	0.368	0.08
2nd - 3rd	18	-2.874	**0.005****	0.40	18	-0.551	0.294	0.19	17	-0.925	0.184	0.43	17	0.000	0.500	0.00	17	-1.820	**0.043***	0.55	17	0.147	0.443	0.04
3rd - 4th	18	3.121	**0.003****	0.48	18	-0.603	0.277	0.16	17	1.434	0.085	0.54	17	0.566	0.290	0.20	17	1.631	0.061	0.35	17	0.539	0.299	0.17
Control - 4th	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	17	-0.954	0.353	0.28	17	0.100	0.922	0.03

Note: Values in each variable (probed movement associated with either a sequence position, 1st - 4th, or a control movement) are the mean raw RTs and error rates per probed position (*Probe* trials). For the adjacent positions t-tests (first three comparisons) the data in the baseline condition were used. The data for the control *vs* the 4th position were averaged across conditions. The first three comparisons are one-tailed tests; last comparison is two-tailed. | * P ≤ 0.05 | ** P ≤ 0.01 | *** P ≤ 0.001 |

Supplemental Table A.S1b | Interaction effects of probed position with preparation duration or sequence timing (4 x 3 repeated measures ANOVAs).

	Experiment 1								Experiment 2								Experiment 3							
	Reaction time (ms)				Press error (%)				Reaction time (ms)				Press error (%)				Reaction time (ms)				Press error (%)			
Interaction	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2
Position × Preparation duration	6	2.069	0.063	0.103	6	3.353	**0.005****	0.157	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Position × Timing	-	-	-	-	-	-	-	-	3.3	2.302	0.082	0.119	6	1.859	0.095	0.099	3.9	0.975	0.426	0.054	6	1.021	0.416	0.057

Note: Dependent measures are the mean raw RTs and error rates (*Probe* trials). | * P ≤ 0.05 | ** P ≤ 0.01 | *** P ≤ 0.001 |

Supplemental Table A.S1c | Main effects of preparation duration or sequence timing on probed movement availability (one-way repeated measures ANOVAs).

	Experiment 1								Experiment 2								Experiment 3							
	Relative RT differences (%)				Relative error differences (%)				Relative RT differences (%)				Relative error differences (%)				Relative RT differences (%)				Relative error differences (%)			
Factor	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2
Preparation duration	2	4.379	**0.020***	0.196	2	3.457	**0.042***	0.161	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Timing	-	-	-	-	-	-	-	-	1.5	0.675	0.475	0.038	2	0.001	0.999	0.00	2	1.918	0.162	0.101	1.3	1.498	0.241	0.081

Note: Dependent measures are the average relative RT and press error differences between the adjacent positions (*Probe* trials). | * P ≤ 0.05 | ** P ≤ 0.01 | *** P ≤ 0.001 |

Supplemental Table A.S2 | Main effects of erroneously pressed position on press rates (one-way repeated measures ANOVAs).

	Across experiments			
	Presses (%)			
Factor	*df*	*F*	*p*	ηp^2
Pressed position when Probe cue: 1st position	2	0.629	0.535	0.012
Pressed position when Probe cue: 2nd position	1.38	84.699	**< 0.001*** **	0.611
Pressed position when Probe cue: 3rd position	1.34	84.903	**< 0.001*** **	0.611
Pressed position when Probe cue: 4th position	1.54	42.948	**< 0.001*** **	0.440

Note: Dependent measures are the incorrect presses per probed position across experiments in percent of all responses (*Probe* trials). | * P ≤ 0.05 | ** P ≤ 0.01 | *** P ≤ 0.001 |

Supplemental Table A.S3a | Correlation analyses of performance with position-dependent differences in movement availability during planning (relative and raw measures).

	Across experiments							
	Relative RT differences (%) [raw RT differences (ms)]				Relative error differences (%) [raw error differences (%)]			
Performance measure	*r*		*p*		*r*		*p*	
Initiation RT	**-0.393**	**[-0.275]**	**0.002****	**[0.021]**	**-0.539**	**[-0.332]**	**< 0.001*****	**[0.007]**
Relative temporal error	**-0.345**	**[-0.335]**	**0.005****	**[0.006]**	-0.051	[0.079]	0.356	[0.284]
Finger error	0.083	[0.064]	0.273	[0.332]	0.118	[0.045]	0.196	[0.372]

Note: Pearson's correlation coefficient was used for the association between relative or raw RT and error differences in the baseline condition (1500 ms; long preparation duration and slow timing conditions in *Probe* trials) and each performance measure. All correlations are one-tailed. | * P ≤ 0.05 | ** P ≤ 0.01 | *** P ≤ 0.001 |

Supplemental Table A.S3b | Main effect of group based on skilled performance on RT and error position-dependent increases, and interaction effects of group with position (mixed ANOVAs).

	Across experiments							
	Reaction time (ms)				Press error (%)			
Factor & Interaction	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2
Group (median split of initiation RT)	1	33.626	**< 0.001*****	0.388	1	10.767	**0.002****	0.169
Position × Group	3	5.700	**0.001*****	0.097	3	3.900	**0.010****	0.069
Group (median split of relative temporal error)	1	0.084	0.773	0.002	1	2.548	0.116	0.046
Position × Group	3	0.471	0.703	0.009	3	2.436	0.067	0.044
Group (median split of finger error)	1	0.270	0.605	0.005	1	1.057	0.309	0.020
Position × Group	3	1.224	0.303	0.023	3	1.453	0.229	0.027

Note: Dependent measures are the mean raw RTs and error rates per probed position in the baseline condition (1500 ms; long preparation duration and slow timing conditions in *Probe* trials). | * P ≤ 0.05 | ** P ≤ 0.01 | *** P ≤ 0.001 |

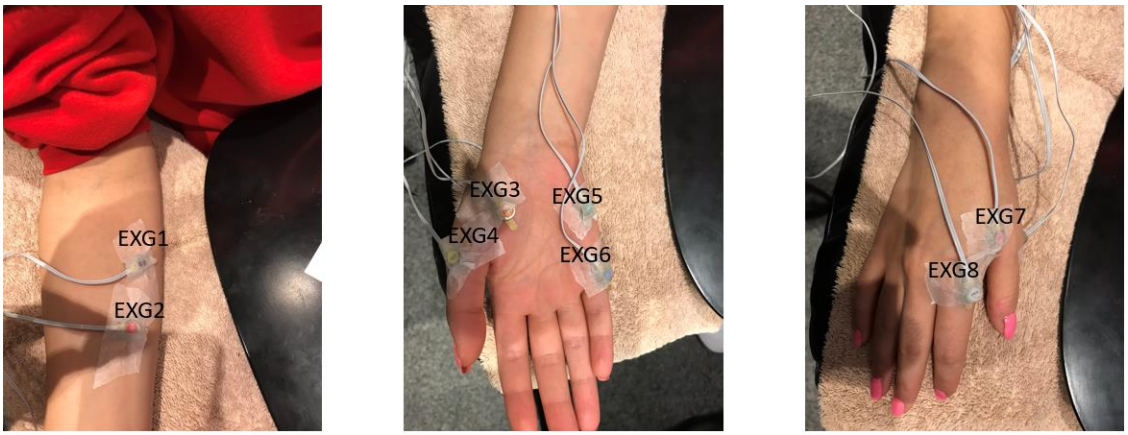
Supplemental Table A.S4 | Main effects of preparation duration and sequence timing on sequence performance (one-way repeated measures ANOVAs), and interaction with inter-press interval position (IPI) (3 x 3 repeated measures ANOVAs).

	Experiment 1															
	Initiation RT (ms)				Relative temporal error (%)				Finger error (%)				Relative timing (% slow)			
Factor & Interaction	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2
Preparation Duration	1.38	52.809	**< 0.001*****	0.746	2	0.105	0.901	0.006	2	0.231	0.795	0.013	-	-	-	-
IPI × Preparation Duration	-	-	-	-	-	-	-	-	-	-	-	-	4	2.528	**0.048***	0.123
	Experiment 2															
	Initiation RT (ms)				Relative temporal error (%)				Finger error (%)				Relative timing (% slow)			
	df	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2
Timing	1.41	1.700	0.207	0.091	2	28.226	**< 0.001*****	0.624	2	0.016	0.984	0.001	-	-	-	-
IPI × Timing	-	-	-	-	-	-	-	-	-	-	-	-	1.26	59.485	**< 0.001*****	0.778
	Experiment 3															
	Initiation RT (ms)				Relative temporal error (%)				Finger error (%)				Relative timing (% slow)			
	df	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2
Timing	1.29	11.590	**0.001*****	0.405	1.45	7.060	**0.007****	0.293	2	0.959	0.394	0.053	-	-	-	-
IPI × Timing	-	-	-	-	-	-	-	-	-	-	-	-	1.56	17.369	**< 0.001*****	0.505

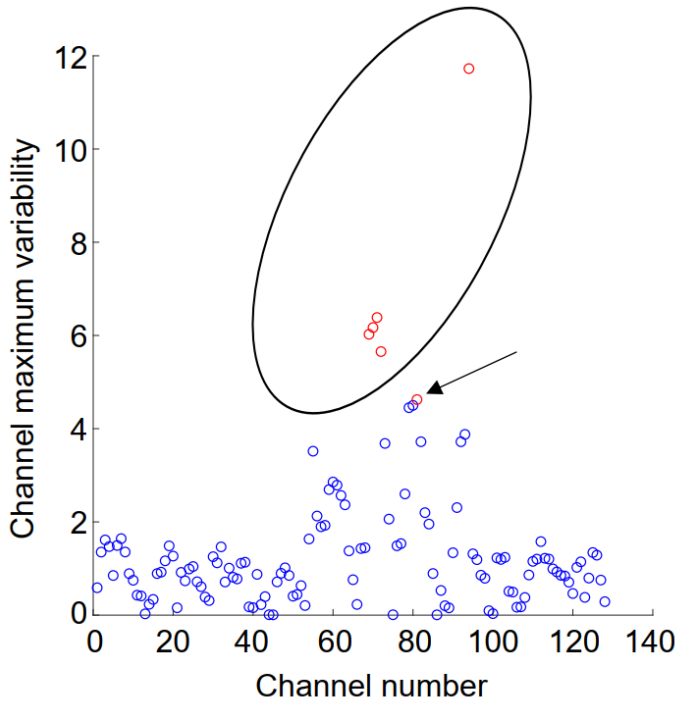
Note: Dependent measures of sequence performance were calculated from the memory-guided *Sequence* trials. Relative timing was quantified relative to the baseline condition (1500 ms; long preparation duration and slow timing conditions). Relative temporal error was the deviation from relative timing from the target IPI. | * P ≤ 0.05 | ** P ≤ 0.01 | *** P ≤ 0.001 |

Appendix B

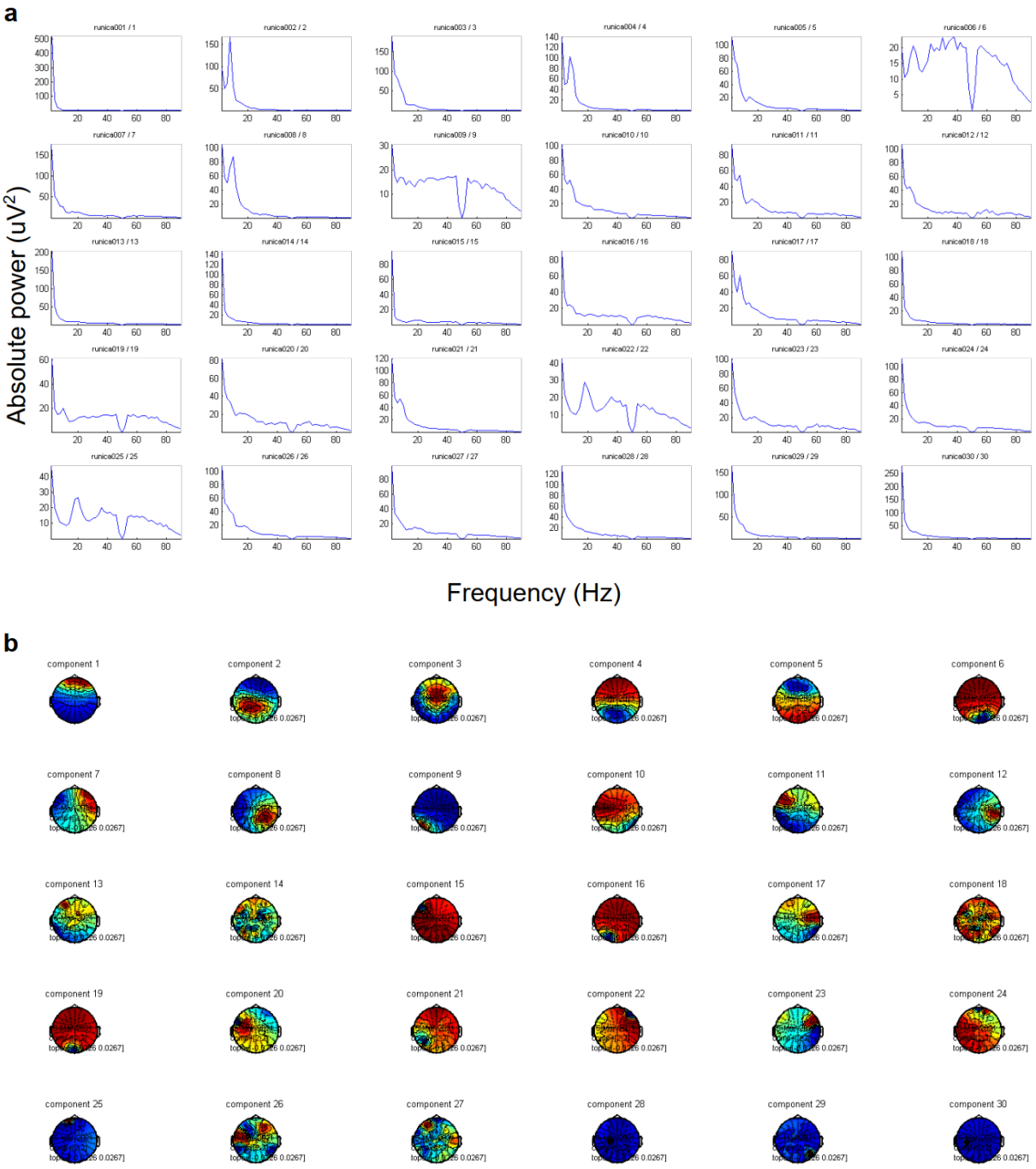
Chapter 3 – Supplemental material



Supplemental Figure B.S1 | EMG electrode setup. Demonstration of surface electrode placement on the right hand/arm of a volunteer. Pairs of electrodes were placed on the same muscle in a bipolar montage: EXG1 and EXG2 on the flexor carpi radialis (arm; left image), EXG3 and EXG4 on the abductor polices brevis (thumb; middle image), EXG5 and EXG6 on the abductor digiti minimi (little finger; middle image), and EXG5 and EXG6 on the first dorsal interrosei (index; right image).

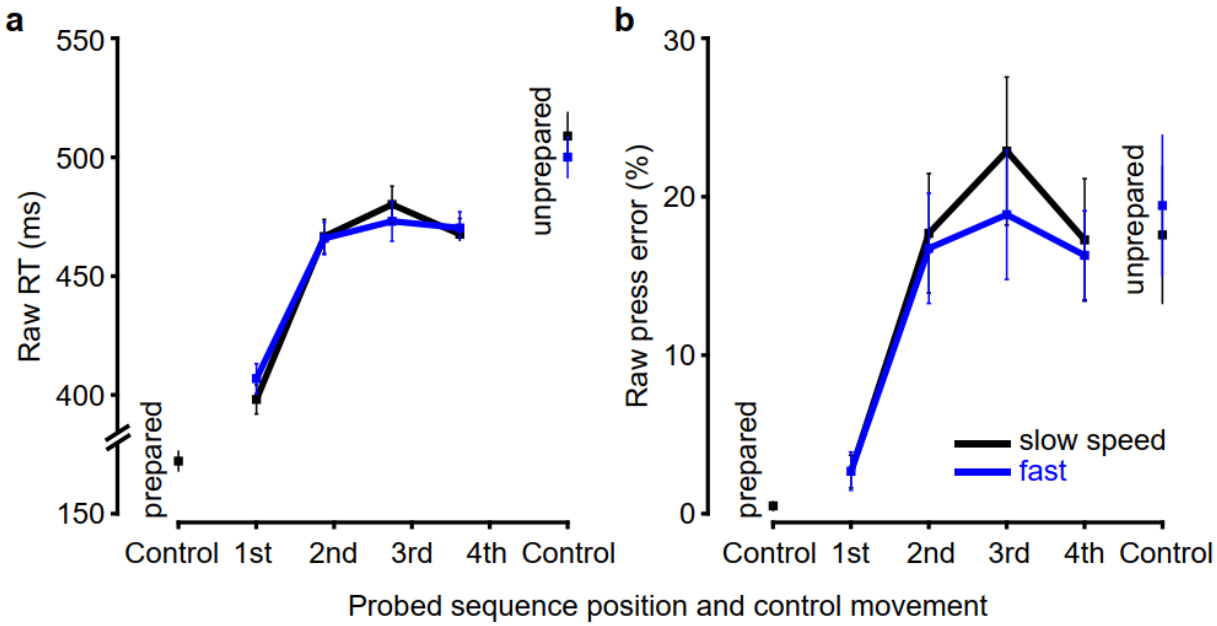


Supplemental Figure B.S2 | Channel outlier detection. Six anterior channels (red circles) were identified as noisy ('outliers') during channel inspection with the Order Statistics based Outlier Detection technique (Giri et al., 2015) in the EEG data of a representative participant. Thorough visual inspection of all trials in each of the detected channels confirmed that five of them accounted for excessive noise (C5, C6, C7, C8, C30 sensors depicted with red circles in the ellipse). Because only a few trials could explain the increased variability of the sixth sensor (pointed with the arrow), it was not marked as a problematic electrode. Channel number in *x* axis refers to the 128 channels used for the EEG recordings. The channel maximum variability on *y* axis refers to each channel's highest variability (see Giri et al., 2015).



Supplemental Figure B.S3 | Activity power spectra and topoplots of independent components. EEG data of a representative participant exhibiting typical blinking and additional noise, especially in A and B sensors. Visual inspection of power spectra (**a**) and respective topoplots (**b**) of thirty ICs indicated increased EMG noise in the occipito-temporal region (see IC6 in **a** and **b**). Low (< 10) B and high (> 25) A sensors accounted for the observed EMG activity as confirmed by cross-checking each channel on a trial-by-trial basis (not depicted here). This artefact was most likely due to contraction of the muscle temporalis or the cervical muscle. After thorough parallel inspection of the ICs' time courses (not shown here) alongside their power spectra and topoplots, components removed were 1, 6, 7 and 15: IC1 due to blinking (C sensors), IC6 due to typical EMG noise as explained above, IC7 due to

noise caused by saccades (C and B sensors), and, last, IC15 due to slow reflex upward eye movements (C and D sensors) typically seen in drowsiness (Bell's phenomenon; Berry, 2012). IC, independent component.



Supplemental Figure B.S4 | Position-dependent movement availability and control movements during sequence planning (raw RT and error rate values). Complementary graphs to Figure 3.2 to illustrate the data used for the corresponding statistical analysis. Raw RT (**a**) and percent press errors (**b**) of probed movements associated with the 1st - 4th press positions of the planned sequence (slow / fast) and of a prepared and unprepared control single movement. Error bars represent standard errors.

Supplemental Table B.S1 | Comparisons for assessing position-dependent increases and control movement availability based on reaction time and press error (paired samples *t* tests) and interaction between sequence position and speed (two-way repeated measures ANOVA).

	Experiment 4							
	Reaction time (ms)				Press error (%)			
Comparison	*df*	*t*	*p*	*d*	*df*	*t*	*p*	*d*
1st - 2nd	17	-7.24	**< 0.001*** **	1.71	17	-4.07	**< 0.001*** **	0.96
2nd - 3rd	17	-1.45	0.083	0.34	17	-1.82	**0.043***	0.43
3rd - 4th	17	1.00	0.166	0.24	17	2.08	**0.027***	0.49
Unprepared - 4th	17	4.90	**< 0.001*** **	1.15	17	1.75	**0.05***	0.41
1st - Prepared	17	22.77	**< 0.001*** **	5.37	17	2.58	**0.01****	0.61
Interaction	*df*	*F*	*p*	*ηp²*	*df*	*F*	*p*	*ηp²*
Position × Speed	3	2.14	0.107	0.11	3	0.48	0.697	0.03

Note: Values in each variable (probed movement associated with a sequence position, 1st - 4th, or a control movement) are the median raw RTs and mean error rates. Data for the probed sequence positions (1st, 2nd, 3rd, 4th) and the Unprepared were averaged across speed conditions. All comparisons are one-tailed.
| * P ≤ 0.05 | ** P ≤ 0.01 | *** P ≤ 0.001 |

Supplemental Table B.S2 | Correlation analysis (Pearson's) between relative RT and error differences and sequence performance.

	Experiment 4			
	Relative RT differences (%)		Relative error differences (%)	
Performance measure	*r*	*p*	*r*	*p*
Initiation RT	0.210	0.202	-0.241	0.167
Relative temporal error	0.302	0.111	-0.053	0.417

Note: Correlations are one-tailed.

Supplemental Table B.S3 | Main effect of group based on skilled performance on reaction time and error position-dependent increases, and interaction of group with position (mixed ANOVA).

	Experiment 4							
	Reaction time (ms)				Press error (%)			
Factor & Interaction	*df*	*F*	*p*	*ηp²*	*df*	*F*	*p*	*ηp²*
Group (median split of initiation RT)	1	6.19	**0.024***	0.28	1	0.04	0.844	0.00
Position × Group	3	0.690	0.561	0.04	-	-	-	-
Group (median split of relative temporal error)	1	0.19	0.668	0.01	1	1.43	0.250	0.08

* P ≤ 0.05 | ** P ≤ 0.01 | *** P ≤ 0.001 |

Supplemental Table B.S4 | Difference of mean relative timing in slow *vs* fast sequence (paired samples *t* tests) and main effects of sequence speed and a single movement on sequence performance (one-way repeated measures ANOVA).

	Experiment 4											
	Relative timing (% slow)											
Comparison	*df*	*t*	*p*	*d*								
Slow - fast (Behavioral)	17	18.36	**< 0.001*** **	4.50								
Slow - fast (EEG)	17	41.73	**< 0.001*** **	9.80								
	Initiation RT (ms)				Relative temporal error (%)				Finger error (%)			
	df	*F*	*p*	*ηp²*	*df*	*F*	*p*	*ηp²*	*df*	*F*	*p*	*ηp²*
Speed (Behavioral)	1.26	263.59	**< 0.001*** **	0.94	1	0.100	0.756	0.006	1	7.94	**0.012***	0.32
Speed (EEG)	2	18.96	**< 0.001*** **	0.53	1	0.001	0.974	0	1	7.3	**0.015***	0.30

Note: Comparisons are one-tailed. | * P ≤ 0.05 | ** P ≤ 0.01 | *** P ≤ 0.001 |

Supplemental Table B.S5 | Comparisons (paired samples *t* tests) for assessing power differences and power changes depending on band x period x movement interaction (2 x 3 x 3 repeated measures ANOVA).

	Experiment 4			
	Power (%)			
Comparisons	*df*	*t*	*p*	*d*
Beta *preparation vs baseline*				
Slow	17	2.66	**0.009****	0.63
Fast	17	2.61	**0.009****	0.62
Single press	17	1.77	**0.048***	0.42
Beta *production vs baseline*				
Slow	17	3.81	**< 0.001*****	0.90
Fast	17	3.95	**< 0.001*****	0.93
Single press	17	2.12	**0.025***	0.50
Alpha *preparation vs baseline*				
Slow	17	-0.14	0.445	0.03
Fast	17	0.41	0.342	0.10
Single press	17	-0.13	0.450	0.03
Alpha *production vs baseline*				
Slow	17	1.89	**0.038***	0.45
Fast	17	2.29	**0.018***	0.54
Single press	17	1.56	0.069	0.37
Interaction	*df*	*F*	*p*	ηp^2
Band × Period x Movement	4	0.65	0.632	0.04
Band x Period	2	3.47	**0.043***	0.17

Note: Comparisons are one-tailed. | * P ≤ 0.05 | ** P ≤ 0.01 | *** P ≤ 0.001 |

Supplemental Table B.S6 | Effect of press position on mean press-related pattern probabilities at the end of preparation period for each modality (one-way repeated measures ANOVA).

	Experiment 4							
	Press-related pattern probabilities (%)							
	EEG				EMG			
Factor: Press position	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2
Slow	4	53.78	**< 0.001*****	0.76	4	0.78	0.544	0.04
Fast	4	32.84	**< 0.001*****	0.66	4	0.96	0.437	0.05

* P ≤ 0.05 | ** P ≤ 0.01 | *** P ≤ 0.001 |

Supplemental Table B.S7 | Effect of press position on mean peak velocity timings for each period and modality (one-way repeated measures ANOVA).

	Experiment 4															
	Peak velocity timings (%)															
	EEG *preparation*				EEG *production*				EMG *preparation*				EMG *production*			
Factor: Press position	*df*	*F*	*p*	*ηp²*	*df*	*F*	*p*	*ηp²*	*df*	*F*	*p*	*ηp²*	*df*	*F*	*p*	*ηp²*
Slow	2	27.23	**< 0.001*** **	0.62	2	12.2	**< 0.001*** **	0.42	2	1.73	0.192	0.09	2	14.97	**< 0.001*** **	0.47
Fast	2	67.08	**< 0.001*** **	0.8	2	15.66	**< 0.001*** **	0.48	2	0.98	0.387	0.05	1.3	29.86	**< 0.001*** **	0.64

* P ≤ 0.05 | ** P ≤ 0.01 | *** P ≤ 0.001 |

Supplemental Table B.S8 | Difference in peak velocity timings between adjacent press positions (paired samples *t* tests) and changes in peak velocity timings of press positions depending on sequence speed (two-way repeated measures ANOVA).

	Experiment 4											
	Peak velocity timings (%)											
	EEG *preparation*				EEG *production*				EMG *production*			
Comparison	*df*	*t*	*p*	*d*	*df*	*t*	*p*	*d*	*df*	*t*	*p*	*d*
Slow												
2nd - 1st	17	4.62	**< 0.001*** **	1.09	17	9.96	**< 0.001*** **	2.35	17	3.22	**0.003****	0.76
3rd - 2nd	17	3.12	**0.003****	0.74	17	2.22	**0.021***	0.52	17	2.80	**0.006****	0.66
4th - 3rd	-	-	-	-	17	1.61	0.063	0.38	17	2.02	**0.03***	0.48
Fast												
2nd - 1st	17	4.36	**< 0.001*** **	1.03	17	19.14	**< 0.001*** **	4.51	17	1.89	**0.038***	0.45
3rd - 2nd	17	9.27	**< 0.001*** **	2.18	17	12.75	**< 0.001*** **	3.00	17	9.59	**< 0.001*** **	2.26
4th - 3rd	-	-	-	-	17	13.45	**< 0.001*** **	3.17	17	3.62	**0.001*** **	0.85
Interaction	*df*	*F*	*p*	*ηp²*	*df*	*F*	*p*	*ηp²*	*df*	*F*	*p*	*ηp²*
Speed x Position	2	3.14	0.056	0.16	1.71	1.35	0.271	0.07	3	1.50	0.226	0.08

Note: Comparisons are one-tailed. * P ≤ 0.05 | ** P ≤ 0.01 | *** P ≤ 0.001 |

Supplemental Table B.S9 | Correlation analysis of EEG peak velocity timings of each press position between preparation and production (pairwise Pearson's correlations).

	Experiment 4	
	Peak velocity timings (%)	
Press position	*r*	*p*
1st	0.359	0.104
2nd	-0.291	0.129
3rd	0.230	0.188

Note: Correlations are one-tailed. Results for the 1st press position are based on $N = 14$, after excluding four outlier subjects.

Supplemental Table B.S10 | Comparisons for assessing EEG single press-related peak velocity timings and pattern probabilities compared to first press position of a sequence (paired samples *t* tests).

	Experiment 4															
	Peak velocity timings (%)															
Comparison	*Preparation - Slow*				*Preparation - Fast*				*Production - Slow*				*Production - Fast*			
	df	*t*	*p*	*d*	*df*	*t*	*p*	*d*	*df*	*t*	*p*	*d*	*df*	*t*	*p*	*d*
1st - single press	17	-0.60	0.560	0.14	17	-0.45	0.658	0.11	17	-1.31	0.208	0.31	17	-1.63	0.122	0.38
	Press-related pattern probabilities (%)															
	Preparation - Slow				*Preparation - Fast*				*Production - Slow*				*Production - Fast*			
	df	*t*	*p*	*d*	*df*	*t*	*p*	*d*	*df*	*t*	*p*	*d*	*df*	*t*	*p*	*d*
1st - single press	17	2.46	0.025	0.58	17	1.34	0.197	0.32	17	2.45	0.026	0.58	17	3.76	**0.002****	0.89

Note: Comparisons are two-tailed and Bonferroni corrected for four tests at $a = .013$.

Supplemental Table B.S11 | Effect of press position on mean peak velocity timings at source level (one-way repeated measures ANOVA), difference in peak velocity timings between adjacent press positions (paired samples *t* tests) and changes in peak velocity timings of press positions depending on sequence speed (two-way repeated measures ANOVA) in each region of interest.

	Experiment 4																			
	Peak velocity timings (%)																			
	M1/S1				PMd				SMA				PhG				DLPFC			
Factor: Press position	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2
Preparation																				
Slow	2	43.81	**< 0.001*****	0.72	2	50.32	**< 0.001*****	0.75	2	33.76	**< 0.001*****	0.67	2	58.28	**< 0.001*****	0.77	2	48.09	**< 0.001*****	0.74
Fast	2	62.94	**< 0.001*****	0.79	2	39.93	**< 0.001*****	0.70	2	51.70	**< 0.001*****	0.75	2	65.09	**< 0.001*****	0.79	2	21.26	**< 0.001*****	0.56
Production																				
Slow	2	7.84	**0.002****	0.32	1.33	3.56	0.062	0.17	2	0.03	0.968	0.002	2	0.01	0.99	0.001	1.26	2.29	0.117	0.12
Fast	2	1.64	0.208	0.09	1.34	1.63	0.212	0.09	2	1.69	0.199	0.09	1.27	5.53	**0.008****	0.25	2	8.14	**0.001*****	0.32
Comparison	*df*	*t*	*p*	*d*	*df*	*t*	*p*	*d*	*df*	*t*	*p*	*d*	*df*	*t*	*p*	*d*	*df*	*t*	*p*	*d*
Preparation - Slow																				
2nd - 1st	17	4.88	**< 0.001*****	1.15	17	3.96	**< 0.001*****	0.93	17	4.37	**< 0.001*****	1.03	17	5.45	**< 0.001*****	1.28	17	5.91	**< 0.001*****	1.39
3rd - 2nd	17	4.98	**< 0.001*****	1.17	17	7.18	**< 0.001*****	1.69	17	4.07	**< 0.001*****	0.96	17	5.47	**< 0.001*****	1.29	17	4.39	**< 0.001*****	1.03
Preparation - Fast																				
2nd - 1st	17	6.97	**< 0.001*****	1.64	17	4.38	**< 0.001*****	1.03	17	4.61	**< 0.001*****	1.09	17	5.86	**< 0.001*****	1.38	17	3.00	**< 0.001*****	0.71
3rd - 2nd	17	4.06	**< 0.001*****	0.96	17	5.08	**< 0.001*****	1.20	17	6.25	**< 0.001*****	1.47	17	5.78	**< 0.001*****	1.36	17	4.67	**< 0.001*****	1.10
Production - Slow																				
2nd - 1st	17	-0.76	0.229	0.18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3rd - 2nd	17	4.38	**< 0.001*****	1.03	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4th - 3rd	17	-1.26	0.112	0.30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Production - Fast																				
2nd - 1st	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	17	-2.81	**0.006****	0.66	17	-3.36	**0.002****	0.79
3rd - 2nd	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	17	2.76	**0.007****	0.65	17	4.37	**< 0.001*****	1.03
4th - 3rd	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	17	1.74	**0.05***	0.41	17	0.53	0.301	0.13
Interaction	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2	*df*	*F*	*p*	ηp^2
Preparation	2	1.24	0.302	0.07	2	0.57	0.571	0.04	1.48	0.39	0.68	0.02	2	0.26	0.776	0.02	2	0.34	0.716	0.02
Production	3	0.32	0.812	0.02	3	0.48	0.645	0.03	1.96	0.39	0.679	0.02	3	2.35	0.084	0.12	3	0.52	0.608	0.03

Note: All comparisons are one-tailed.| * P ≤ 0.05 | ** P ≤ 0.01 | *** P ≤ 0.001 |