ABSTRACT

Title of Dissertation:	MENTAL WORKLOAD AND PERFORMANCE DYNAMICS UNDERLYING HIERARCHICAL PLANNING PROCESSES DURING COMPLEX ACTION SEQUENCE EXECUTION UNDER VARIOUS DEMANDS
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Mental workload arises from the link between task demands and the engagement of processing resources. While mental workload has been studied extensively, only a limited body of work has examined this notion as it relates to the generation of discrete, goal-oriented action sequences which are critical to most daily activities (e.g., making a cup of coffee). Such action sequences engage high-level (cognitive) processes to plan the order of actions in combination with low-level (sensorimotor) processes for movement execution. The study of this hierarchical mechanism is important to inform how action sequences governed by a goal and rules are generated such that some are more parsimonious (e.g., fewer actions) than others. In such a context, the examination of mental workload could further characterize the engagement of high- and low-level processing resources along with their interaction to face cognitive and sensorimotor demands. Although prior efforts have examined discrete action sequence performance, they did not study mental workload

dynamics via a combined assessment of complementary neurophysiological correlates (i.e., regional activity, functional connectivity) while simultaneously manipulating both cognitive and motor demands to characterize the relationship between high- and low-level processing resources. Further, most prior action sequence studies overlooked the functional interaction between regions thought to be critical for coordinating these high- and low-level processes such as the dorsolateral prefrontal (dlPFC), premotor (PMC), and sensorimotor (SMC) cortices. Also, most of these studies were clinical without considering healthy individuals or computational tools that can assess in detail the structure of the performed action sequences. Therefore, through a combined evaluation of performance and brain dynamics, this work aimed to examine the engagement of high- and low-level processing resources underlying mental workload when individuals execute action sequences under varying cognitive and motor demands. In the present study, participants solved an action sequence task (Tower of Hanoi) under normal (i.e., physical) and altered (i.e., virtual) sensorimotor conditions and low and high cognitive demand. Performance was examined using task completion time and sequence structure (Levenshtein distance). Regional EEG power activity along with functional connectivity between the dlPFC, PMC, and SMC were used to evaluate cortical effort and cortico-cortical communication in the theta, low-alpha, and high-alpha bands. Sensorimotor mu-rhythm, frontal theta/parietal alpha (FTPA), and frontal theta/frontal alpha (FTFA) power ratios were also computed. Results revealed larger task completion time, elevated EEG power in all three frequency bands in the anterior-frontal and occipital regions, enhanced temporal theta and low-alpha power, and attenuated mu-rhythm during the normal relative to the altered sensorimotor conditions. Cortico-cortical communication between the dlPFC and both the PMC and SMC increased with cognitive demand under the normal but not altered conditions. Further, larger task completion time and Levenshtein distance were associated with enhanced theta power in the

anterior-frontal, frontal and occipital regions, increased FTFA ratio, and larger functional theta connectivity as cognitive demand increased. Findings indicate degraded performance along with increased mental workload as revealed by greater recruitment of cognitive-motor resources in response to increased cognitive demand and under normal relative to the altered conditions suggesting that the former imposed larger sensorimotor demands compared to the latter. Connectivity results suggest resources may, to some extent, be shared when facing combined elevation of cognitive and motor demands and highlight the PMC's role in the low- and high-level interface for action sequence execution. These results may inform applications related to physical and/or virtual execution of action sequence tasks such as, but not limited to, rehabilitation, human factors, and human-robot interactions.

MENTAL WORKLOAD AND PERFORMANCE DYNAMICS UNDERLYING HIERARCHICAL PLANNING PROCESSES DURING COMPLEX ACTION SEQUENCE EXECUTION UNDER VARIOUS DEMANDS

by

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Dissertation submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
2025

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Acknowledgements

First and foremost, I would like to thank my adviser, Dr. Rodolphe Gentili, for his mentorship, leadership, and support throughout my time at Maryland. I am sincerely grateful to have had the opportunity to learn from and work with you over the last few years. Thank you for all of the early mornings and late night meetings and for always keeping my best interest in mind. I would also like to thank my committee members, Dr. Bradley Hatfield, Dr.Immanuel Samuel, Dr. Donald Bolger, and Dr. Hyuk Oh for their guidance and expertise. Their feedback was instrumental in the completion of my Ph.D. dissertation. I would further like to thank Dr.Hyuk Oh for all of his technical support. I am truly fortunate to have been able to learn so much from each of you outside of this project, thank you all so much.

I would like to thank my parents, Jodi and Russell Shaver, and my sister, Rachel Shaver, for their unwavering love and support. Mom and dad, I am so thankful to you both for always encouraging me, being there when I needed anything, and for constant pictures of the pups. I couldn't have done this without you.

I would also like to thank my lab members and UMD colleagues for their constant support and friendship. Jayesh, Kyle, Gabe, and Catherine, thank you all for everything from help with data collection and stats all the way to Looney's. This would have been infinitely harder without you.

Lastly, I would like to acknowledge and thank all of the students, faculty, and staff of the Department of Kinesiology their support.

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Chapter 1: Introduction

Mental workload

Definition and theoretical frameworks

Mental workload (MWL) is a multidimensional construct used to describe the relationship between the imposed task demands and the corresponding neural resources allocated to address the associated high-level cognitive processes (e.g., attention, inhibition, working memory) as well as the low-level sensory (e.g., proprioception) and motor (e.g., motor coordination) processing demands. While no generalizable, objective measure of MWL has been identified, attempts at fully characterizing the concept have been made using various tools, theories, models, and frameworks of human cognition (Longo et al., 2022). The classic and often-cited early work is that of Kahneman (1973), who proposed a limited capacity model of attention referred to as the single resource model. In this model, attention is viewed as one whole single, finite, pool' of resources that can be allocated as necessary to achieve, maintain, or improve task performance as time-on-task increases and adjusted if task demands change or are not as expected. According to this framework, when two or more tasks are performed concurrently, impaired performance of one or both tasks (i.e., task interference) depends on the demands imposed by each task individually. When task demands drain the 'pool' of resources, performance of one or both tasks suffers. On the other hand, when demands are below resource capacity, the 'pool is full' of unengaged resources that can be allocated to maintain or improve performance (Kahneman, 1973; Norman & Bobrow, 1975). 'Automated' tasks are those that minimally engage neural resources,

leaving more to attend to unexpected stimuli (Fitts & Posner, 1967; Schneider, 1985). Automation of a skill is generally the result of practice or exposure to a task facilitating more efficient resource allocation strategies such as the ease with which experienced performers adjust to task demands compared to novices (Hatfield, 2018; Miller et al., 2011; Rietschel et al., 2014). Thus, the ability to simultaneously perform two separate tasks, or tend to multiple task components, depends on effectively allocating resources to task-relevant processing.

While intuitive, research at the time revealed that variance in dual-task performance could not be attributed strictly to the difficulty of the individual tasks/components nor to the resource allocation policy between tasks (i.e., which task is 'favored' and which is 'neglected'), limiting the applicability of the single resource model. Instead, results implied that differences in the demands placed on the anatomical structures responsible for information processing led to the differences in performance, behaving as if they were supported by multiple separate, but still finite, resources (Wickens, 2002, 2008; Wickens & Llu, 1988). Thus, the multiple resources theory was proposed to provide a framework for predicting the interference of tasks or task components based on the idea that humans have separate neural resources that can be recruited for information processing (Wickens, 2002, 2008). That is, resource competition is not for the structures themselves but instead for the resource(s) responsible for engaging and enabling these structures. According to the multiple resources theory, separate resource pools exist along four dimensions each with distinct levels and physiological mechanisms: i) processing stages, ii) perceptual modalities, iii) visual channels, and iv) processing codes. According to this model, these four

components functionally engage separate pools of resources for response selection and execution. The processing stages dimension first addresses perceptual and cognitive activities and implies they involve the same resources. The latest addition to the model that complements more recent models of working memory is the processing code dimension which indicates that spatial activity and verbal/linguistic activity employ different resources for perception, working memory, and action (Baddeley, 2012; Wickens, 2008; Wickens et al., 1983). The separation of spatial and verbal resources seemingly accounts for the relatively high degree of efficiency with which manual (i.e., motor) responses that are spatial in nature and vocal/spoken responses which are verbal in nature can be done simultaneously (Wickens & Llu, 1988). So, according to this updated model, manual control may disrupt performance in a task environment by imposing demands on spatial working memory (Baddeley, 2012; Wickens, 2008; Wickens et al., 1983). In the case of resource sharing such as this, overloading resources (i.e., draining the pool) can occur and generally impairs performance as there are not enough resources available to address all task demands (Baddeley, 2012; Wickens & Boles, 1983; Wickens, 1976, 1980, 2002; Wickens & Llu, 1988). Practically, this implies that more information can be processed simultaneously when separate modalities are involved.

Similar to the single resource model, limitations of the multiple resources theory include the challenge of estimating a 'baseline' level of task demand since the level of demand also depends on the experience and characteristics of individuals, making it difficult to use dual-task paradigms to measure resource engagement (Wickens et al., 1983). Additionally, this model assumes that resources will be

deployed logically and optimally towards the primary task or its primary component, which is not guaranteed, especially in situations of over or underloading (e.g., under-engaged drivers prioritizing phone conversation over road safety). It has also been suggested that this model does not properly address the presence of general resources that are available to and demanded by all tasks, modalities, codes, and stages (Seeber, 2007). This means that the multiple resources theory alone cannot explain the role or activation level of the resources engaged or their hierarchy in a cognitive-motor context. In summary, although MWL has been widely examined, due its multidimensional and complex nature, the hierarchy that dictates resource engagement and allocation is not well understood.

Mental workload and performance

In the context of task performance, a large body of work has demonstrated that as task demands increase, the engagement of neural resources also increases to maintain performance, resulting in higher levels of MWL. An excessive increase in MWL (i.e., overloading) can impair processing efficiency by effectively draining one's resource pool, leaving an insufficient amount available to address unexpected events or novel stimuli, possibly leading to catastrophic errors and even injury (Dyke et al., 2015; Gentili et al., 2011, 2014; Miller et al., 2014; Rietschel et al., 2012; Shaw et al., 2018; Wickens et al., 1983). However, if some processing resources remain available, this reserve can be used to maintain performance when task demands change (Cheng et al., 2015; Dehais et al., 2020; Fitts & Posner, 1967; Murray & Hunfalvay, 2017; Murray & Janelle, 2007). Importantly, even if performance is maintained, an increase in MWL inherently results in reduced cognitive-motor efficiency (Neubauer & Fink, 2009)

which describes the relationship between performance and MWL (Hatfield, 2018; Jaquess et al., 2018; Pashler, 1994; Rietschel et al., 2014; Shuggi et al., 2017, 2018, 2019). Therefore, MWL and performance dynamics are primary drivers of cognitive-motor efficiency and critical to consider when assessing adaptive cognitive-motor behavior (Young et al., 2015).

Cognitive, motor and sensory task demands, environmental influence, situational factors, subjective feelings, effort, individual differences, strategy, and practice/experience are thought to impact MWL (DiDomenico & Nussbaum, 2008; Kantowitz, 1987; Longo et al., 2022). These factors and/or their combinations can change the levels of attention, effort, and arousal of an individual, ultimately impacting what is required to maintain performance. For example, in addition to overload situations, underloading these resources can also impair performance due to a mismatch between demands and capabilities or excessive automation (Byrne & Parasuraman, 1996; Strayer & Drews, 2007; Strayer & Johnston, 2001). Together, these factors simultaneously encourage and discourage the use of different performance strategies by individuals to cope with task demands. For example, some highly fatigued individuals may omit or ignore task components while others may alter their strategy to avoid such errors (e.g., slow down). In turn, further modifying task demand and ultimately impacting neural resource engagement. As such, it is difficult to estimate how non-linear resource engagement relates to the coping strategies employed by individuals during cognitive-motor tasks as well as their unconscious physiological underpinnings without utilizing a combination of metrics that include performance,

subjective, and physiological measures; however, this type of combined approach is uncommon (Longo et al., 2022).

Neural correlates of mental workload

MWL has been investigated using various subjective measures, performance metrics, and different physiological markers, however, a prior review suggested that only 11% of the literature employed a combination of these three classes (Longo et al., 2022). Currently, the most common survey used for subjective MWL assessment is the NASA task load index (TLX) (Grier, 2015; Hart, 2006; Longo et al., 2022). The six subscales include: mental demand, physical demand, temporal demand, perceived performance, effort, and frustration. Although scores are often or averaged together, individual subscales are commonly considered (DiDomenico & Nussbaum, 2008). In particular, it has been suggested that the mental demand dimension is most relevant to MWL assessment in a cognitive-motor context as mental demand was correlated to neurophysiological data (Akizuki et al., 2015; Shaw et al., 2018; Shuggi et al., 2019).

Regarding neurophysiological markers, neuroimaging methods such as functional near infra-red spectroscopy (fNIRS) and electroencephalography (EEG) are two promising methods for MWL assessment as they allow for continuous monitoring of neurophysiological mechanisms during tasks without detrimentally interfering with the possible task execution strategies (i.e., neither restrict movement excessively). For example, EEG-based metrics in the time (e.g., event related potential -ERP- amplitude) and frequency (e.g., spectral power) domains, and more recently functional connectivity (Guan et al., 2022; Kakkos et al., 2019) have been employed to assess MWL and cortical engagement during task performance under different levels of task

demand (Allison & Polich, 2008; Blanco et al., 2016; Gentili et al., 2014, 2018; Gevins & Smith, 2000, 2003; Miller et al., 2014; Shaw et al., 2018; Ullsperger et al., 2001). These prior studies have also largely examined spectral power in two EEG frequency bands specifically, theta (4 − 8 Hz) and alpha (8 – 13 Hz), as their relationship with cortical engagement and inhibition has been identified in many scenarios including memory (Klimesch, 1999) and attention (Clayton et al., 2015; Kazemi 2020). This is consistent with the notion that cortical oscillations in the theta and alpha frequency bands are thought to reflect signals arising from distinct subregions of thalamus that can in turn be modulated by the frontal cortex which is critical for high-level processes such as memory and attention (Ketz, 2015).

Generally, changes in the theta frequency band are thought to reflect the recruitment or engagement of attentional resources for working memory, action/error monitoring, and concentration in cognitive and motor tasks (Coombes et al., 2005; Gentili et al., 2011, 2014; Gevins & Smith, 2000, 2003; Hsieh & Ranganath, 2014; Jaiswal et al., 2010; Klimesch, 1999; M. W. Miller et al., 2014; Miyata, 1990; Slobounov et al., 2000). For example, increases in fronto-medial theta power have been observed prior to accurate performance on prolonged cognitive tasks (Esterman et al., 2013; Oehrn et al., 2014) and after the occurrence of motor errors (i.e., speed focused) and cognitive errors (i.e., accuracy focused) tasks (Cavanagh et al., 2012; van Driel et al., 2012). This increase in theta power has been observed with reduced alpha power in task-relevant cortical areas (Mazaheri et al., 2009). Activity in the alpha frequency band, often split into low-alpha (~8-10 Hz) and high-alpha (~11-14 Hz), is thought to represent cortical inhibition meaning an increase of alpha (and particularly high-alpha)

power would reflect more inhibition (i.e., less engagement) of cognitive-motor resources during task performance (Klimesch, 2012; Klimesch et al., 2007). This is supported by several prior EEG studies which examined cortical dynamics while manipulating the level of cognitive-motor challenge and found that as task demands increase, low-alpha (~8-10 Hz) and high-alpha (~11-14 Hz) power were attenuated. The observed reductions of low- and high-alpha would reflect increased general arousal and increased recruitment of task-specific resources, respectively (Klimesch, 1999; Klimesch et al., 2007; Shaw et al., 2019). Additionally, some work has challenged the traditional view that theta strictly represents the number of items being held in working memory. More specifically, theta oscillations may reflect preparation for allocating attention between multiple task-relevant sensory modalities (i.e., visual and auditory) as variations in theta power were observed as the number of sensory modalities to be attended to changed, not strictly with the number of items held in working memory. Further, alpha oscillations were thought to suppress task-irrelevant visual information during trials requiring participants to attend to auditory information specifically and therefore may represent actively ignoring specific sensory input. Based on these results, it was suggested that the relationship between fronto-midline theta and posterior alpha reflect processes was specifically related to multisensory-divided attention (Keller et al., 2017a).

Alpha over the sensorimotor cortex is referred to as the mu frequency bandwidth (Pfurtscheller & Aranibar, 1977). It has been suggested that mu reflects the activation of cortical areas for processing sensory and cognitive information for the production of motor commands, modulates the integration of a new ability during

motor skill acquisition, and is associated with expertise development in a motor-related task (Brunsdon et al., 2020; Cannon et al., 2014; Orgs et al., 2008; Pfurtscheller, 1992). A decrease in mu power is interpreted as the involvement of a larger neural network or more cell assemblies for information processing (Pfurtscheller & Lopes Da Silva, 1999). This is supported by work which typically revealed a reduction in mu during tasks involving sensorimotor processes (Friesen et al., 2017). As such, mu could indicate the size of the neural network recruited for task performance and is a useful measure of neural resource engagement in the context of cognitive-motor tasks with different sensorimotor and cognitive demands (Inamoto et al., 2023).

It has been proposed that cortico-cortical communication within different EEG frequency bands reflects the activation and functional couplings of the underlying cortical structures and can also be used to detect changes in MWL (Rietschel et. al., 2012). A measure of cortico-cortical communication which is less common but quickly gaining popularity is functional connectivity analysis (Guan et al., 2022; Ismail & Karwowski, 2020; Longo et al., 2022). Functional connectivity metrics identify statistical (undirected) associations among spatially distinct brain regions. Prior research has shown that as task demand and MWL increase, the functional integration of brain regions tends to increase to address increased processing demands (Dai et al., 2017; Ismail & Karwowski, 2020; Taya et al., 2016). This is thought to be supported by the cognitive control network as connectivity within the cognitive control network in both the theta and alpha frequency bands tend to have shorter characteristic path lengths and higher global efficiency under high levels of MWL, implying that interactions are reinforced to allow information transfer across the whole network in

order to successfully address task demands (Guan et al., 2022b). This is supported by research showing increased theta synchronization in response to conflict during action monitoring (Oehrn et al., 2014) and increases in cognitive-motor task demands (Gentili et al., 2018b; Miller et al., 2011, 2014; Rietschel et al., 2012; Shaw et al., 2018, 2019). Interestingly, a study using modified Simon tasks revealed that trials during which accuracy was prioritized over speed were characterized by less error-related theta power, an absence of error-related theta phase synchronization between the medial and dorsolateral prefrontal cortex, stronger error-related suppression of parieto-occipital alpha power, and stronger parieto-occipital–frontal alpha synchronization compared to trials during which speed was emphasized or when equal emphasis was placed on accuracy and speed (van Driel et al., 2012). This is in line with the model proposed by Clayton and colleagues (2015) which suggests that connections between the medial PFC and lateral PFC are facilitated by long-range phase synchronization in theta and connections between the lateral PFC and posterior sensorimotor regions are also enhanced by phase synchronization in the fronto-posterior network in frequencies lower than 14 Hz, such as alpha and theta. In the context of cognitive-motor control, theta and low- and high-alpha functional connectivity increases with task demand (Rietschel et al., 2012; Shaw et al., 2019). Along these lines, decreased alpha functional connectivity has been observed in response to increased cognitive demand possibly to facilitate the engagement of task-relevant brain regions (Dai et al., 2017). As such, decreased functional connectivity in the alpha and theta frequency bands likely reflects efficient cognitive-motor processing.

In sum, using EEG to assess cortical engagement and cortico-cortical networking affords temporal resolution without restricting participants' movement. This allows for the examination of MWL in a variety of situations including ecologically valid paradigms such as, but not limited to, dual-task walking, virtual environments, driving, and aircraft flight control (Allison & Polich, 2008; Chuang et al., 2013; Coombes et al., 2005; Gentili et al., 2014, 2018; Scheer et al., 2016; Shaw et al., 2019). In the context of cognitive-motor performance, spectral power and functional connectivity changes within the theta and alpha/mu bandwidths have been observed under different levels of demand in various tasks including computer-based, cognitive-motor tasks using wet and dry EEG systems and appropriately reflect MWL (Gentili et al., 2018; Guan et al., 2022; Rietschel et al., 2012; Shaw et al., 2018, 2019). Finally, the use of a neurophysiological assessment combined with performance and subjective measures is rare but allows for a comprehensive evaluation of cognitive-motor efficiency which describes the relationship between MWL and performance (Hatfield, 2018; Longo et al., 2022; Shuggi et al., 2019).

Complex action sequences

Definition

For the purposes of the current study, complex action sequences are defined as those which: **i)** generate high cognitive-motor demands in novices (e.g., high-level planning, working memory, attentional control), **ii)** require a substantial amount of practice to be mastered, **iii)** involve several degrees of freedom and substantial hand-eye coordination, and **iv)** are relevant to human behavior in real-world settings (Hauge

et al., 2019, 2021; Katz et al., 2017; Wulf & Shea, 2002). These complex action sequences differ from action sequence tasks typically used in research which **i)** tend to be more sensorimotor in nature, **ii)** generally involve a simple goal with stringent success criteria (i.e., limited degrees of freedom) and, **iii)** consist of a continuous and overlapping series of sub-elements (e.g., sequential finger tapping or pressing key buttons) that are arbitrarily related to each other (Gale et al., 2022; Huberdeau et al., 2019; Kansaku et al., 2004). This distinction is important because many activities of daily living are composed of complex action sequences that require various degrees of both cognitive and motor control including constraints on how to execute the sequence. The remainder of this document will focus on this type of action sequence that meets the four criteria mentioned first in this section. In the case of such complex action sequences, individual actions are influenced by various rules, enforced externally by the environment/task or implicitly by the individual, ultimately requiring a number of intermediary, discrete steps to be completed in an appropriate order that is influenced by behaviors prior to and following the current state. In the context of activities of daily living, such as making a cup of coffee, performing surgery or brushing teeth, complex action sequences are associated with a multitude of appropriate and inappropriate strategies with varying levels of efficiency and effectiveness. In many cases, the order of some steps is critically important for successful task completion (e.g., getting a cup is required before pouring the coffee), while the order of other steps can be changed at the individual's discretion (e.g., sugar can be added to the cup before or after the coffee). This discretion is afforded by higher-level processes which support successful implementation of an appropriate action sequence by developing flexible planning

strategies based on the identification of critical aspects of a task and a desired end-state, which are then enacted by the lower-level processes (Naylor & Briggs, 1963). Therefore, understanding the neurophysiological mechanisms that support the ability to plan and execute appropriate action sequences under such conditions is a critical step towards improving safety and satisfaction in many contexts (e.g., rehabilitation, assistive devices, human-machine interaction).

Traditional Tower of Hanoi

The Tower of Hanoi (ToH) puzzle and its variations (e.g., Tower of London) are examples of well-established complex action sequence tasks that have been used to examine high-level processes in a way that is comparable to daily tasks. The traditional ToH (Figure 1) has been used for decades by researchers and clinicians to assess executive function in clinical populations and more recently in healthy adults to assess cognitive-motor mechanisms and MWL related to complex-action sequence execution and practice under different conditions (Ceja, 2019; Ceja et al., 2018; Goel & Grafman, 1995; Griebling et al., 2010; Hauge et al., 2019, 2021; Milla et al., 2019; Shaver et al., 2023; Shuai et al., 2017; M. C. Welsh et al., 1999; Yu et al., 2016). The ***objective*** of the traditional ToH task is to move 2-8 disks (initially stacked in order of diameter with the smallest on top) from the leftmost peg to the rightmost peg in as few moves as possible while following ***three task rules*****: i)** only one disk can be moved at a time, **ii)** a disk may not be placed on the table or held with the other hand while another disk is being manipulated, and **iii)** a larger disk cannot be stacked on top of a smaller disk (Figure 1). Importantly, no matter how many disks are involved or what the initial-state and end-goal states are, the ToH rules result in only one possible 'optimal' solution. The

optimal solution being defined here as the action sequence composed of the minimum number of moves required to achieve the desired end-goal state. Importantly, there are still many appropriate 'sub-optimal' solutions with varying degrees of efficiency (i.e., executing more moves to achieve the same goal). Though seemingly simple, determining the optimal action sequence, or even just an appropriate action sequence, requires the engagement of high-level processes. This is supported by a large body of work showing activity (or lack thereof) in the prefrontal cortex (PFC), particularly the dorsolateral PFC (dlPFC), related to solving ToH puzzles. Manipulating a traditional wooden ToH puzzle also requires fine motor-control of the digits, an ability that relies on low-level processes and may additionally tax resources normally associated with executive function (Fine & Hayden, 2022; Rigoli et al., 2012; Taylor & Ivry, 2014). Therefore, like many activities of daily living, the ToH requires both low- and high-level processing, especially when individuals are naive to the task.

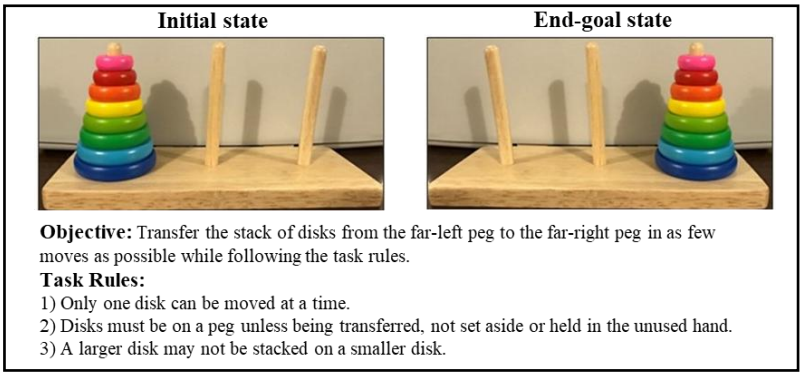

Figure 1: Traditional Tower of Hanoi (ToH) puzzle composed of a wooden board, three evenly spaced pegs, and eight wooden disks stacked leftmost peg.

To summarize, there are several major advantages to using the ToH to examine cognitive-motor performance including: engagement of high-level (cognitive) and low-level (motor) requirements also imposed by many activities of daily living, it requires

fine motor control specifically, performance can be measured objectively due to always having only one 'optimal' solution and many sub-optimal solutions, the dlPFC is a known contributor to successful performance, difficulty can be adjust easily, and it is novel to most individuals. However, until recently, ToH performance has been assessed using relatively simple metrics (e.g., completion time) that do not detail the quality of the performed action sequences (Hauge et al., 2019, 2021; Katz et al., 2017; Shaver et al., 2023). Further, how physical ToH puzzles compare to virtual ToH puzzles in the context of neural resource allocation strategies remains unclear as virtual ToH puzzles (e.g., tablet and computer-based puzzles) have long been used in place of physical puzzles with a few more recent studies research suggesting neurological differences when individuals use different ToH systems (Ceja et al., 2018; Milla et al., 2019).Thus, the ToH is a valid tool for better understanding neural resource allocation strategies related to high- and low-level processing that support cognitive-motor performance in a relatively ecological manner.

Traditional and computational ToH performance measures

Similar to activities of daily living, complex action sequences can be completed successfully in multiple ways but only a few or even only one 'optimal' solution exists. Such is the case for the traditional ToH which has many sub-optimal solutions but always has only one 'optimal' solution that minimizes the number of moves needed to reach the same goal end-state. ToH studies generally report fairly simple metrics such as completion time, number of puzzles completed, the total number of moves, number of backwards or reversal moves, or the number of errors made (Ceja et al., 2018; Goel & Grafman, 1995; Noyes & Garland, 2003; Rinehart et al., 2006; Saint-Cyr et al., 1988;

Steenbergen & Gordon, 2006). Additionally, some studies have examined the 'pause time' before beginning a ToH puzzle and between moves as it has been suggested that these pauses may reflect the underlying processes, specifically working memory (Welsh et al., 1995). It seems that when performing a 4-disk ToH (the optimal solution involving 15 actions), compared to poor performers, optimal and self-correcting performers increase their pause time before three configurations that are known challenge points: the 1st, 5th, and particularly the 9th move of the optimal sequence when using a physical puzzle (Welsh et al., 1995). In an earlier study which employed a computer model of the 3- and 5-disk ToH, found that the longest pause time occurred before the first move and this seemed to reduce pause time between moves when the minimum number of moves was used to solve the puzzle and was accompanied by reduced pause time before move one in subsequent trials (Karat, 1982). Importantly, the first move is when just under 50% of errors were made despite having the longest pause time and still did not predict ToH performance; but, considered together, pause times at moves one, five, and nine differ for optimal, self-correcting, and poor performers and therefore together may contribute to enhanced performance (Spitz et al., 1985; M. ; Welsh et al., 1995; Welsh, 1991; Welsh & Huizinga, 2005). The observed disconnect between move one pause time and ToH performance could not be explained by individuals knowledge of the advantages of planning a sequence before beginning action execution as interview data suggested individuals with poor and self-correcting performance use planning strategies in a similar manner compared to optimal performers (Cavanaugh & Perlmutter, 1982; Welsh et al., 1995; Welsh, 1991). It was suggested that this disconnect may reflect the quality of the planning strategies

and/or the load placed on working memory (Carpenter, 1990; Welsh et al., 1995; 1991; 1999), which, in the case of the ToH involves processing and storing of information related to the identification of subgoals, generated moves/sequences and their execution, monitoring the results of said execution, and revision of plans as necessary (Welsh et al., 1995). Importantly, the aforementioned studies included children of different ages and cognitive statuses as well as adults and all presented with these temporal and error patterns. While informative, these do not provide detailed information about the actual sequence of actions executed by poor and self-correcting performers who were compared to the optimal performers. Assessment of the action sequence structure in this manner is critical for examining the quality of the high-level processes in particular (Hauge et al., 2019, 2021; Katz et al., 2017; Shaver et al., 2023). Additionally, while the degree of optimality in performance has been described computationally for low-level sensorimotor processes using kinematics and kinetics (e.g., minimization of the jerk, torque, torque change, etc.), computational approaches for assessing the optimality of high-level processes are sparse (Anderson et al., 2005; Goel & Grafman, 1995; Hinz et al., 2009; Rinehart et al., 2006).

To address this gap, a recent series of studies applied Levenshtein Distance algorithm to complex action sequences (Hauge et al., 2019, 2021; Katz et al., 2017; Shaver et al., 2023). Levenshtein distance represents the number of alterations needed to transform one sequence into another by incorporating three operators: the number of insertions, deletions, and substitutions present in a sequence (e.g., sequence performed by an individual) compared to a reference sequence, for example, the shortest possible sequence (Levenshtein, 1966). The number of insertions operator describes the addition

of a new action at any position in the sequence, increasing the length of the performed sequence by one compared to the reference sequence. The number of deletions operator describes the removal of an action at any position in the sequence, decreasing the length of the performed sequence by one compared to the reference sequence. The number of substitution operator describes the replacement of an existing action with a new action at a given position in the sequence, leaving the performed sequence length unchanged compared to the reference (Ho et al., 2017; Levenshtein, 1966; Shaver et al., 2023; Wagner & Fischer, 1974). More differences between the performed and reference sequence would result in a higher/larger Levenshtein distance which would indicate that the performed sequence deviates from the reference sequence. Importantly, in the context of complex action sequences, incidences of any of these operators potentially impacts the following actions in a meaningful way. For example, the optimal (i.e., shortest) ToH sequence requires the first action to be correct. If the individual makes a substitute at this point, it is impossible to solve the puzzle in the minimum number of moves. Thus, Levenshtein distance can quantify the degree of optimality of a performed sequence to achieve a goal (Hauge et al., 2019, 2021; Katz et al., 2017; Shaver et al., 2023). Also, Levenshtein distance and its operators have been combined with measurements of MWL to assess changes in cognitive-motor efficiency during the imitation of different complex action sequences (Hauge et al., 2019). Therefore, using a computational approach based on Levenshtein distance to examine changes in the structure of goal-oriented action sequences is useful for understanding the relationship between sequence structure (i.e., high-level processes) and MWL under various experimental conditions.

Empirical work related to hierarchal mechanisms of cognitive-motor control

A growing body of research suggests that cognitive-motor control is a complex hierarchical mechanism that simultaneously, not separately, engages the high-level (i.e., cognitive) processes responsible for abstract human behavior along with the low-level (i.e., sensorimotor) processes responsible for implementing movements specified by the high-level processes (Sober & Sabes, 2003, 2005). High-level processes are critical for determining an appropriate order for sequentially executing a complex series of discrete actions to reach a (Fabbri-Destro et al., 2009; Wilmut et al., 2013). More specifically, high-level processes engage core executive functions (e.g., inhibition; (Diamond, 2013) to determine and monitor behavior based on task characteristics and the desired end-goal state goal (e.g., sequence of actions to prepare a meal using the least amount of dishware). At the same time, low-level processes generate movement parameters and implement these actions (Casartelli et al., 2017; Rosenbaum et al., 2012; Rosenbaum et al., 2018). Importantly, these two processing levels, whether separate pools or not, are linked in that the encoding of feedback from lower-level processes by higher-order processes reciprocally supports the reorientation of parameters by lower-level processes during ongoing and future task performance (Casartelli et al., 2017). That is, low-level processes support adjustments to future movements as well as ongoing movements in the presence of immediate changes in task demand as any feedback perceived during or after task execution that prompts alterations to one or more actions would need to be accounted for by higher-level cortical areas in order to appropriately update the action(s), sequence order, and/or the

goal (C. Wu, 2007). In support of this notion, when healthy individuals execute tasks that require manual dexterity, executive function seems to explain a portion of variance in fine motor performance, hinting at its associations with high-level functions (i.e., response planning, working memory, and cognitive flexibility which is also referred to as set-shifting) (Rigoli et al., 2012; Stöckel et al., 2017; Stöckel & Hughes, 2016; Stuhr et al., 2018). More generally, it appears that different motor skills engage very specific cognitive control processes and that the activation of brain regions critical to executive functioning is positively associated with the novelty and complexity motor tasks (Stuhr et al., 2018). This is consistent with the notion that while separate cognitive control processes would be deployed for both cognitive and motor task, to some degree, it would also be shared (Leisman et al., 2016; Feolo et al., 2023; Marvel et al., 2019). This idea of a close link between high- and low-level processes is supported by prior work which proposes that the initiation of each level is related to the challenges associated with the physical space and the intricacy of the motor task (Longo et al., 2022; Stuhr et al., 2018). For instance, if one wants to make a glass of water and the cup is initially upside down, grasping the cup in a way that leaves it upside down may be a simple movement when considered alone but will require a second movement to properly prepare/place the cup. Instead, inversion of the hand when picking up the cup, correcting its orientation, reflects the prioritization of 'end-state comfort' as the goal and 'rules' dictate that the cup should be right-side up in order to be used (Rosenbaum et al., 2018). This is in line with Baddeley's model of working memory (Figure 2) which includes a primary component—the central executive—and three sub-components thought to be responsible for the temporary storage and manipulation of

information (Baddeley, 2012). The sub-components include: the phonological loop for storing speech-based information, the visuo-spatial sketchpad for storing visual images and spatial information, and the episodic buffer for storing integrated episodes and "chunks" from perception and long-term memory. According to this model, the central executive coordinates the allocation and re-allocation of resources to each of the sub-components based on task demand and the goal using a combination of top-down and bottom-up signaling.

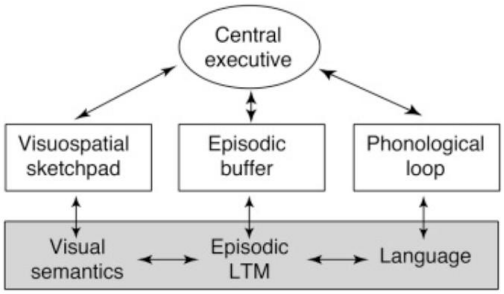

Figure 2: Baddeley's model of working memory (borrowed from Baddeley 2012). LTM = long term memory.

The PFC is a reasonable candidate for the central executive described in Baddeley's model because the PFC is known to be essential for executive functions (e.g., shifting of attention, updating and monitoring of information, and inhibition of prepotent responses) and the activity of PFC neurons correlates with perception as well as action, suggesting that it houses representations of sensory states, actions and their combinations (Asaad et al., 2000; Duff et al., 2011; Fuster, 2015; Matsumoto & Tanaka, 2004; Miller et al., 1993; Nagel et al., 2005; Stuhr et al., 2018). Moreover, successful simple motor sequence learning after stroke has been associated with PFC network activation (Alkon et al., 1991; Buonomano & Merzenich, 1998). Additionally, the PFC is clearly involved in sensorimotor control and learning (Floyer-Lea &

Matthews, 2004, 2005; Gentili et al., 2011; Shadmehr & Holcomb, 1997) especially during the early stages of learning (Gentili et al., 2011; Seidler & Noll, 2008). Further, a shift from the engagement of the PFC to the parietal regions has been observed in sequence learning (Sakai et al., 1998). This is supported by anatomical evidence confirming that the PFC receives low-level information from sensory association cortices but not from the primary sensory cortices, and the PFC sends information to motor association cortices such as the supplemental motor areas (SMA) and premotor (PM) cortices (Kim et al., 2018). This suggests the PFC plays a prominent role in the coordination and exchange of information and its central location facilitates its influence over the operations of other cortical and subcortical areas via top-down signaling (Duff et al., 2011; Fuster, 2015; Kantowitz, 1987). Such a dynamic functionally translates into a hierarchical and bidirectional relationship between high-level processes (e.g., defining the goal state, determining an appropriate order of actions) associated with the PFC and low-level sensorimotor processing in which the primary motor (M1) cortices, PM cortices, and the SMA play critical roles (Baddeley, 2012; Kim et al., 2018; Wu, 2017).

The dlPFC and the anterior cingulate cortex are thought to support adaptive modification of ongoing processes and increasing cognitive control by engaging attentional resources as necessary (Clayton et al., 2015; Dehais et al., 2020; Gevins et al., 1997). Activity of the left dlPFC has been implicated in the identification of information relevant to goals and the creation of an internal problem representation, while the right dlPFC has been associated with mental transformations and working memory (Ruocco et al., 2014; Song et al., 2020). In clinical populations, connectivity

between the dlPFC and other cortical areas has been investigated using simple and complex finger tapping sequences (Anwar et al., 2016), motor imagery and execution (Kim et al., 2018), set-shifting (Sadaghiani et al., 2019), and working memory (Axmacher et al., 2008). Another study compared the connectivity of the dlPFC in healthy young and older individuals performing spatially coupled and decoupled finger tapping tasks (Loehrer et al., 2016). Regarding healthy populations, dlPFC connectivity has been examined in the context of visual information processing using transcranial magnetic stimulation (Kazemi et al., 2020), planning of different reaching motions with different types of feedback (Le et al., 2022), and cognitive reappraisal under different levels of stress (Al-Shargie, 2021). While most of this work was conducted using aging, lesion, and stroke paradigms, taken together, they provide evidence not only that the integrity of dlPFC is important for cognitive-motor performance, but also that functional relationships with other cortical areas may be related to the employment of strategic high- and low-level processes that support successful task execution (Clayton et al., 2015; Kazemi et al., 2020; Palva & Palva, 2011; Sadaghiani et al., 2019; Schulz et al., 2019; Taylor & Ivry, 2014). It has been suggested that the dlPFC contributes to cognitive control by transmitting top-down signals to bias information flow across task-relevant sensory and motor areas (Miller & Cohen, 2001; Sadaghiani et al., 2019). This would be accomplished through increased synchronization in the alpha frequency band, which relies on the dlPFC, temporally aligning excitability cycles across distant brain regions to segregate blocks of information and facilitate or inhibit communication/connectivity between regions within different frequency such as theta (Clayton et al., 2015; Kazemi et al., 2020; Palva & Palva, 2011; Sadaghiani et al.,

2019). The results discussed above support the recently proposed idea that the PFC is akin to the premotor cortices (Fine & Hayden, 2022) and that cognitive and motor processes are engaged together during successful cognitive-motor performance (Melnik et al., 2017; Stuhr et al., 2018). This supports the hypothesis that the sensorimotor contingencies housed in the centrally-located PFC inform high-level functions such as flexible cognitive control. These results also support the idea of a complex hierarchical mechanism that places high- and low-level processes on a cognitive-motor continuum rather than fully separating them. Thus, collectively, prior behavioral and neurophysiological work suggest the role of the PFC, particularly the dlPFC, as the central executive responsible for coordinating high- and low-level processing to appropriately allocate neural resources under different circumstances (Asaad et al., 2000; Averbeck et al., 2006; Baddeley, 2012; Duff et al., 2011; Matsumoto & Tanaka, 2004; Miyake et al., 2000).

This relationship between high- and low-level processes and the role of the dlPFC specifically in coordinating task-relevant sensory and motor information is in line with several views of sensorimotor integration that propose an intimate relationship between sensory and motor processing with cognition. For example, according to the embodiment thesis about cognition; cognition, the body, and context exist as a whole rather than separately, emphasizing the implied role of the body for reenactments of the brain's modality-specific systems for perception and action rather than emphasizing the body's direct role. That is, it suggests that perception guides motor actions and motor actions influence perception (Foglia & Wilson, 2013). Along these lines and related to the multiple resource theory, the common-coding approach proposes the

existence of overlap between afferent and efferent codes instead of a separate-coding-and-translation approach (Prinz, 1992, 1997). In addition, sensorimotor contingency theory links action, perception, and object recognition to the cortical activity present during exploratory object manipulation (Nagel et al., 2005). In support of these, it was proposed that sensorimotor independent components, or 'modules', are active during both perception and response execution under different levels of processing demand (Melnik et al., 2017). These results suggest that low- and high-level planning are related to each other such that sensorimotor processing demand is in fact wholly sensorimotor processing rather than separate sensory and motor processing. However, it was noted that similar numbers of sensorimotor, motor, and sensory modules were identified suggesting that activation of functional modules in sequence (rather than together) supports the transition of sensory input to motor output—in line with the time-sharing aspects of resources described by Wickens (Wickens, 2002, 2008). This leaves the impact of different sensorimotor processing requirements, such as the use of virtual compared to physical systems, on neural resource allocation policies related to high- and low-level processing unclear. Although some work has investigated the relationship between the high- and low level-processes, to our knowledge, no study manipulated both high and low processing levels simultaneously to investigate the concurrent variations of MWL and performance during the execution of complex action sequences. Understanding the functional organization of this complex, hierarchal mechanism by examining regional activity and functional connectivity of the dlPFC is critical for interpreting the graded and multidimensional nature of human cognitive-motor control and MWL.

Complex action sequences, mental workload, and cognitive-motor planning

Many studies have examined complex action sequence performance using the ToH which engages both high- and low-level processing due to the rules of the task and the manual dexterity required to execute the associated movements. Unsurprisingly, different ToH protocols (e.g., different number of disks, colors, sizes, goal states, etc.) consistently revealed engagement of the PFC, including the anterior, inferior and dorsolateral regions. Importantly, most of these studies focus mainly on clinical populations (Ceja et al., 2018; Fabbri-Destro et al., 2009; Naylor & Briggs, 1963; Ruocco et al., 2014; Wilmut et al., 2013) and performance assessment included fairly simple metrics that do not detail the quality of action sequences generation (e.g., number of moves, number of puzzles completed) (Noyes & Garland, 2003; Radüntz, 2020). In addition, to the lack of more advanced performance assessment methods, MWL was not examined through a combined assessment of regional cortical activity or cortico-cortical communications in relation to sequential task performance along with subjective measures of MWL. For instance, to our knowledge, only a few studies have examined the concomitant changes in performance and MWL by combining a novel computational approach (i.e., using the Levenshtein distance) and a well-established survey (i.e., NASA TLX), respectively (Hauge et al., 2019, 2021; Shaver et al., 2023). Although these studies employed a more advanced computational method for performance assessment, cortical dynamics, which can objectively assess changes in MWL, were not examined. Therefore, a limited effort has examined MWL dynamics during the execution of action sequences in healthy or clinical populations, but no prior

work has examined the cognitive-motor processes underlying MWL using complementary neurophysiological measures along with a computational method that characterizes performance success by quantifying sequence structure.

Although the neural mechanisms underlying complex action sequence execution have been investigated, a limited number of studies have examined the relationship between the high- and low-level processing systems and their contribution to MWL. While research supports the PFC's role in the strategic deployment of high- and low-level processes during action sequence execution, most of this work was conducted using, aging and lesion studies which potentially induce bias due to their specificities (Piek et al., 2004, 2007; Rahimi-Golkhandan et al., 2015; Schulz et al., 2019; Stuhr et al., 2018; Taylor & Ivry, 2014; Tisseyre et al., 2018). Only a small body of work has examined MWL dynamics present when healthy individuals execute (i.e., performance settings) or practice (i.e., learning settings) ToH sequences (Ceja et al., 2018; Hardy & Wright, 2018; Hauge et al., 2019, 2021; Katz et al., 2017; Milla et al., 2019; Radüntz, 2020; Shaver et al., 2023). Therefore, there is a need to consider healthy individuals. Along these lines, previous work has suggested that complex action sequence performance in young healthy individuals is affected by the training conditions such that variation enhances the internal task representations thought to be housed in the PFC (Borys et al., 1982; Noyes & Garland, 2003; Schiff & Vakil, 2015; Vakil & Heled, 2016; Welsh, 1991; Welsh & Huizinga, 2005). For example, in one study, during initial task performance where the weight of each ToH disk matched its size (i.e., the smallest disk weighed the least and each larger disk weighed increasingly more), participants were then asked to explain their performance and the amount of

gesturing done by the individual participants during their explanation was recorded. After explaining their initial performance, they were asked to perform the ToH again. One group used the exact same puzzle (i.e., the weight of each disk matched the diameter). A second group used a different ToH puzzle with the disk weights reversed (i.e., the smallest disk weighed the most and each larger disk weighed less). Worse performance during the reverse-weight ToH trial was correlated with the amount of gesturing done when explaining initial ToH performance such that more gesturing associated with worse performance with the reverse-weight puzzle (Beilock & Goldin-Meadow, 2010). This implies that if the mental representations are incompatible with action parameters (i.e., low-level processes), problem-solving (i.e., high-level processing) suffers.

Several prior investigations have employed virtual ToH systems in place of physical systems, assuming that they engage comparable neural mechanisms, which evidence suggests may not be the case as differences in performance (Noyes & Garland, 2003) and PFC activation have been observed (Ceja et al., 2018a; Milla et al., 2019). In healthy individuals, those who used a 3D physical ToH puzzle before attempting a 2D virtual ToH puzzle had a significant reduction in cortical activation of the prefrontal regions during their second attempt compared to individuals who completed the 2D virtual trials first (Milla et al., 2019). Importantly, both groups (groups were based on which ToH puzzle was attempted first: 2D virtual or 3D physical) improved performance (i.e., increased the number of puzzles completed) and neural efficiency (i.e., reduced activity of the dlPFC) in block 2 compared to block 1—but improved performance and neural activation was only associated with individuals

that began with the physical puzzle. The authors suggest that prior explicit knowledge of the puzzle solution obtained during initial trials reduced participants' cognitive load leading to improved performance during later trials in all participants regardless of the initial modality (i.e., 2D or 3D puzzle) in accordance with several other works (Kalyuga et al., 2004; Naylor & Briggs, 1963; Sweller, 2008; Taylor, 2013). However, sensorimotor and cognitive demand were not systematically manipulated (e.g., participants completed 3-disk ToH using the 3D system followed by a 4-disk puzzle using the 2D system), leaving their contribution to the observed differences in performance and neural resource engagement unclear. Still, these results are in line with sensorimotor adaptation study results demonstrating that individuals who utilize explicit knowledge of perturbation characteristics are able to more rapidly reduce errors during reaching movements compared to participants who do not exhibit this same level of explicit knowledge (de Brouwer et al., 2018, 2022; Fernandez-Ruiz et al., 2011; Welsh & Huizinga, 2005). Regarding sensorimotor manipulation, it seems that different combinations of sensory feedback differentially engage the sensorimotor cortex (SMC), PMC, and the PFC, as correlations between PFC activation and activation of the other two regions can be modulated by specific sensory input combinations (Zheng et al., 2023). Also, using the ToH puzzle, another study determined that the short-term plasticity of the representations of the fingers in primary somatosensory cortex was regulated by a prefrontal–cortical sensory gating system (Schaefer et al., 2005).

In the aforementioned ToH study by Milla and colleagues (2019), the correlation between improved performance and improved cortical efficiency was only

observed in participants that used the 3D physical puzzle first but performance was similar to those who used a 2D puzzle first. More specifically, neural efficiency analysis revealed that the increase in efficiency was five times greater in participants who initially attempted the 3D physical puzzle compared to participants that started with the 2D virtual puzzle. This difference was attributed to the increased complexity of the 3D physical puzzle imposing higher motor and/or cognitive load during initial trial, which in turn increased the neuroplastic changes across the cognitive-motor network(s) supportive of learning and transfer (Ceja et al., 2018a; Noyes & Garland, 2003a; M. C. Welsh & Huizinga, 2005a). This is in line with the results of another previously discussed study (Beilock & Goldin-Meadow, 2010) that found that gesturing was related to ToH performance and performance quality decreased when the low-level processing was different in subsequent ToH trials. Additionally, individuals with different levels of developmental coordination disorder exhibited differences in cortical activation while using a physical ToH but not a virtual 2D version of the ToH when compared to healthy individuals (Ceja et al., 2018a). Further, though not statistically significant, participants achieved better Levenshtein distance, along with statistically better sequence completion times using a virtual ToH compared to participants who performed their trials using a physical ToH (Shaver et al., 2023). This is interesting because differences between physical and virtual systems could be attributed to the fact that during physical execution of the ToH, the high- and low-level processes are naturally linked whereas during virtual execution these two processing levels are artificially decoupled. Unfortunately, none of these studies systematically

manipulated the cognitive and sensorimotor demands imposed by the ToH so the link between high- and low-level processes remains unclear.

In summary, a large body of work supports the idea of cognitive-motor control existing on a continuum rather than separately but the contribution of high- and low-level processes to cortical engagement and cortico-cortical communication is not well understood especially in the context of complex action sequence execution. Further, evidence supports the notion that explicit knowledge of both cognitive and physical aspects of a task/environment facilitates performance while a mismatch impairs performance (Beilock & Goldin-Meadow, 2010b; de Brouwer et al., 2018b). Further, more recent research has shown that initial attempts at the ToH using the 3D puzzle, while physically more demanding, led to better neural efficiency in subsequent trials compared to initially attempting the 2D puzzle (Milla et al., 2019a; Noyes & Garland, 2003a). However, none of the aforementioned studies combined cortical regional activity and cortical networking with more advanced analysis of high-level performance using computational tools while systematically manipulating task demands. Therefore, the functional relationship between the high- and low-level processes and the resulting neural resource allocation policies that support complex action sequence execution have not been fully characterized. As interest in virtual/remote options across many domains (e.g., stroke rehabilitation, human-machine interaction) continues to rise, it becomes increasingly important to understand the implications of increasing or reducing sensorimotor processing demand on cognitive-motor efficiency, learning, and the transfer of skill.

Aims and significance

Objective

The ability to plan goal-oriented complex action sequences to achieve a goal is critical for most activities of daily living. While informative, the previous body of work concerned with MWL in the context of action sequences has not yet fully characterized the link between high- and low-level processes. Collectively these studies: **i)** did not examine the differences in MWL related to high- and low-level processing demand using a combined assessment of objective, subjective, and complementary neurophysiological correlates (i.e., regional cortical activity and functional connectivity; Longo et al., 2022), **ii)** largely examined clinical populations with a limited focus on healthy individuals, **iii)** did not examine the quality of high-level performance in a detailed manner, **iv)** mostly involved simple sequential tasks (e.g., sequential keyboard strokes) that were largely motor in nature and which do not aim to solve a problem, and **v)** did not examine the functional role of the dlPFC in coordinating the high- and low-level processes that support cognitive-motor performance along with the resulting subjective MWL. As a result, the neural resource allocation strategies related to high- and low-level processing, the functional relationships between the dlPFC and task-relevant cortical areas, as well as the subsequent impact on cognitive-motor performance and subjective MWL remain unclear in the context of ecologically valid complex action sequences. To address these gaps, the overarching objective of the current study is to better understand the relationship between high- and low-level processing and the subsequent subjective and objective MWL by characterizing the neural resource allocation strategies present during complex action sequence execution.

This was done using a combined assessment of participants' performance in a traditional manner (i.e., sequence completion time, cognitive and motor sequence completion time components, and number of puzzles completed), performance specifically related to the high-level processing (Levenshtein distance), cortical effort (EEG spectral power), cortico-cortical networking dynamics (EEG functional connectivity), as well as, subjective MWL during complex action sequence execution that is similar to activities of daily living (i.e., ToH) under different cognitive task demands.

Specific aim 1 and hypotheses

Specific aim one was to examine performance and regional cortical activity during the execution of complex action sequences with different levels of cognitive demand under normal and altered sensorimotor conditions. In the physical world, complex action sequences are executed with a natural coupling between high- and low-level processes that determine and execute an appropriate action sequence. In many cases, fine motor control of the hands is required to manipulate relevant task components (e.g., disk manipulation during ToH puzzles) and may engage resources normally associated with high-level processes such as working memory and attention (Fine & Hayden, 2022; Rigoli et al., 2012; Taylor & Ivry, 2014). As such, successful action sequence performance is supported by appropriately allocating neural resources to the high-level cognitive processes, as well as, to the lower-level sensorimotor processes, especially when the task is novel and fine motor control of the digits is needed. Therefore, it is reasonable to expect that fewer cognitive resources would be required if the complexity of sensorimotor coordination is reduced. This

‘*simplification*’ would result in a reduction of MWL (i.e., reduction neural resource engagement) and an increase in the amount of reserved resources that could then be (re)allocated to the high- and low-level processes to maintain or optimize cognitive-motor performance and/or address adverse or unexpected levels of task demand (Jeffri & Rambli, 2021; Noyes & Garland, 2003; Wickens, 2008). Therefore, our primary hypothesis is that, compared to the normal condition, a beneficial simplification of low-level sensorimotor processing would result in: **i)** better performance as indexed by a greater number of completed puzzles, faster sequence completion, and lower Levenshtein distance, **ii)** lower MWL as indicated by efficient cortical engagement/effort (i.e., lower theta, enhanced low-alpha, high-alpha power, as well as lower frontal-theta / parietal-alpha and frontal-alpha/ frontal-alpha ratios) and, **iii)** enhanced mu power during the altered relative to the normal conditions.

Alternatively, the alteration of the low-level sensorimotor processes may not result in a ‘*simplification*’ but instead perturb the natural coupling between high- and low-level processes used by default in the normal condition ultimately leading to impaired performance and an elevation of MWL. If this is the case, compared to the normal condition, such an alteration of the low-level processing will result in: **i)** a decrease of performance as indexed by a lower number of completed puzzles, slower sequence completion, and a greater Levenshtein distance, **ii)** an elevation of MWL as indexed by greater theta, lower low-alpha and high-alpha power, as well as, greater frontal-theta / parietal-alpha and frontal-alpha/ frontal-alpha ratios), and **iii)** reduced mu power during the altered relative to the normal conditions. Importantly, these differences in performance and MWL are expected to be more pronounced under high

levels of cognitive task demand (i.e., when participants are asked to solve more complex ToH puzzles) which further consume cognitive resources compared to lower-demand tasks suggesting the use of executive resources would be shared for both cognitive and sensorimotor demands. If these executive resources are independently allocated for the cognitive and sensorimotor demands, thus the differences in performance and cortical dynamics due to sensorimotor requirements will not be modulated by the cognitive demand. Lastly, an elevation of MWL was expected under greater cognitive demand for both the normal and altered conditions.

Specific aim 2 and hypotheses

Specific aim 2 was to examine cortico-cortical communication patterns, as well as subjective MWL during the execution of complex action sequences with different levels of cognitive demand under normal and altered sensorimotor conditions. Based on the literature discussed above, the dlPFC plays a critical role in high-level processes and possibly low-level processes (Fine & Hayden, 2022; Rigoli et al., 2012; Taylor & Ivry, 2014). While the PMC and SMC are critical for low-level processes, including fine motor control of the hands. Additionally, the PMC has been suggested to support high-level processes (Bonini et al., 2010; Fine & Hayden, 2022; Rizzolatti et al., 2002; Schulz et al., 2019). However, the hierarchical nature of their relationship remains unclear in the context of goal-oriented complex action sequences which depend on both processing levels. Therefore, considering these three regions (i.e., dlPFC, PMC, SMC; M. D. Byrne, 2001; Ritter et al., 2019; Trafton et al., 2013) and following the same reasoning as specific aim 1, the same two alternative hypotheses were considered for the functional relationship of these regions in addition to subjective MWL. Specifically,

our primary prediction was that simplifying low-level processing would reduce functional communication (i.e., cortico-cortical networking) between the dlPFC and both the PMC and SMC and result in reduced subjective MWL. More specifically, the simplification of low-level processing was expected to produce: **i)** reduction of functional connectivity (i.e., decreased Weight Phase Lag Index (WPLI) values) between the dlPFC and the other two regions (PMC and SMC) in the theta, alpha, mu, low-alpha and high-alpha frequency bandwidths, **ii)** lower subjective MWL as indexed by lower NASA TLX scores and, **iii)** reduced functional connectivity (i.e., decreased WPLI values) between the SMC and the PMC in the theta, alpha, mu, low-alpha and high-alpha frequency bandwidths.

Alternatively, modifying the low-level processing may disrupt the natural coupling between high- and low-level processes ultimately increasing cortico-cortical networking and perceived MWL. In this case, it is reasonable to expect an increase in functional communication and perceived levels of MWL as individuals attempt to maintain performance under these unusual conditions. Such strategies would likely result in: **i)** an increase of functional communication between the dlPFC and the two other regions (PMC and SMC) in the bandwidths of interest, **ii)** an increase in perceived MWL, and **iii)** elevated cortico-cortical communication between the PMC and SMC.

As for specific aim 1, if cognitive control processes are shared for both cognitive and motor demands, the differences in connectivity dynamics due to sensorimotor requirements should be modulated by the cognitive demand otherwise it would suggest that they are rather separated. Finally, an elevation of MWL was expected as cognitive demand increase for both normal and altered conditions.

Significance

As previously discussed, the ability to plan and execute appropriate complex action sequences to reach a goal (e.g., make a sandwich) is critical to everyday life. In such cases, high-level processes determine an appropriate sequence of actions while low-level processes execute said actions. However, the link between these processing levels remains unclear. From a basic science standpoint, the results of the current study can contribute to better characterization of the cognitive-motor resource deployment strategies that support the formulation and execution of complex action sequences, improving our understanding of the interplay between high-level (cognitive) and low-level (sensorimotor) processing. From an applied perspective, understanding the neurocognitive processes that support the rehabilitation, acquisition, automation, and transfer of skills remains one of the most important topics to be investigated. Since physical and virtual systems afford different constraints and sensorimotor inputs, the use of both while also manipulating the cognitive aspects of a task allows for direct examination of the relationship between high- and low-level processing. Therefore, the results of the current study may inform the development of more impactful in-person and remote rehabilitation and training protocols that utilize physical and/or virtual systems. Within the field of human factors, neuroergonomics focuses on the investigation of the neural bases of mental functions and physical performance. In this context, bridging the gap between neural correlates and MWL would be a useful tool in the design of human-machine interfaces that optimize workload. Additionally, beyond the fields of human neuroscience and human factors, this work aims to characterize efficient coupling of sensorimotor and cognitive processes that support the

performance of goal-oriented complex action sequences. This could inform the development of advanced adaptive control architecture, potentially improving applications related to cognitive robotics.

Chapter 2: Methods

Participants

Twenty-five participants were recruited for the present study. However, three participants were excluded as they did not execute the task properly at all and/or demonstrated a lack of understanding of the task (i.e., rule breaks and drops > 25% of total trials). Therefore, data from 22 participants between the ages of 18-35 years old (Female = 14; Age = 21±3.1) were analyzed and included here. All were healthy without any known neurological impairments or musculoskeletal injuries that restrict upper-limb movement. All reported normal or corrected-to-normal vision and were right-handed as determined by the Edinburgh Handedness Inventory. Additionally, all participants scored within or above the 'typical' range on the commonly used mini mental state exam indicating no major cognitive impairments were present. Participants also completed demographics questionnaires regarding their general experience with logic/mathematical puzzles, computer-based games, and with the ToH specifically. Only self-described ToH beginners without knowledge of the traditional ToH rules and with limited logical/mathematical puzzles and computer game experience were included. Though all participants used a computer mouse in the present study, they also indicated their preference for trackpads compared to a computer mouse. All participants confirmed that no alcohol or other substances that may impact the central nervous system were ingested within 24 hours of participation. All participants provided informed consent by signing the document approved by the University of Maryland IRB before answering any questionnaires or beginning any trials. A statistical power analysis was performed to identify the minimal sample size. The

power analysis was executed with a significant threshold of $\alpha = 0.05$ along with a power of 0.80 and a medium effect size for a within-subject analysis and resulted in a sample size of N = 21 (G*Power 3.1). To account for possible data loss, 25 participants were collected but only 22 were included in the analysis.

Experimental task and design

Experimental task: Modified Tower of Hanoi

The ToH is a mathematical puzzle that has been used for decades as a neuropsychological tool for assessing executive function in healthy and clinical populations (Ceja et al., 2018; Goel & Grafman, 1995; Griebling et al., 2010; King et al., 2021; Shuai et al., 2017; Welsh et al., 1999; Yu et al., 2016). The traditional ToH task includes three identical, evenly spaced pegs in a straight line and begins with 2-8 disks stacked on the far-left peg in order of diameter such that the largest disk is on the bottom and the smallest is on top (see Figure 1). Adding more disks is the most common way cognitive task demand is manipulated as it exponentially increases the minimum number of moves required to reach the desired end-goal state (i.e., increases the complexity of the optimal solution). Additionally, the starting position of the disks or the goal end-state can be adjusted without changing the optimal solution. Therefore, like many activities of daily living the ToH can be presented with different initial conditions (e.g., starting with the stack of rings on the far-right; Peg C) and desired end-goal states (e.g., stack of rings on the middle peg; Peg B) while maintaining only one optimal solution (i.e., shortest action sequence).

As such, the present study included low and high cognitive demand conditions with 3 and 4 disks, respectively (Figure 4). These were chosen because 5 disks would likely have been too difficult for most participants to complete in the allotted time (3 minutes) despite being young and healthy. However, the 3-disk ToH is fairly simple and as such the healthy, young participants considered here may disengage. To mitigate this, participants were asked to complete a modified version of the ToH for the low and high cognitive demand conditions. More specifically, for both cognitive demand conditions, participants were required to reach an intermediate-goal state (i.e., sub-goal; stack on Peg B or C) before reaching the end-goal state (i.e., stack on Peg A on the far-right) which would then count as a completed puzzle (Figure 3). It is important to note that the task objective was to move the stack of disks from the starting peg to the sub-goal peg and back to the starting peg (i.e., complete a puzzle) in as few moves as possible for the duration of the 3-minute trial and without breaking the traditional ToH rules: **i)** only one disk can be moved at a time, **ii)** disks cannot be stored on the table or in the other hand and, **iii)** a larger disk cannot be placed on top of a smaller disk. To encourage active problem solving, as well as mitigate practice effects and boredom, the sub-goal was switched after each low and high cognitive demand trial. The reference sequence— 'optimal' solution with the minimum number of moves/actions was N=14 and N=30 for the low and high cognitive demand conditions, respectively.

For all low and high cognitive demand trials, the initial and goal states were the same: disks stacked in order of diameter with the smallest disk on top and the largest on the bottom of Peg A (far-left). For all conditions, regardless of the number of disks

or the sub- and end-goal states, there was only one 'optimal' solution (i.e., reference sequence) that consisted of the minimum number of moves/actions required to complete a ToH puzzle while still abiding by the aforementioned rules. Before each trial, participants were asked to sit in their standardized 'ready' position: feet on the ground, facing forward, non-dominant hand stabilizing the ToH system, and their dominant hand resting on the table. They were allowed to begin after the researcher said 'Go' and were stopped after 3 minutes. Before beginning any trials, participants were told what to do if a disk was dropped and what would happen if they broke a task rule. During trials, participants were prompted by the researcher to correct any rule breaks that were not self-corrected and (See Performance section below).

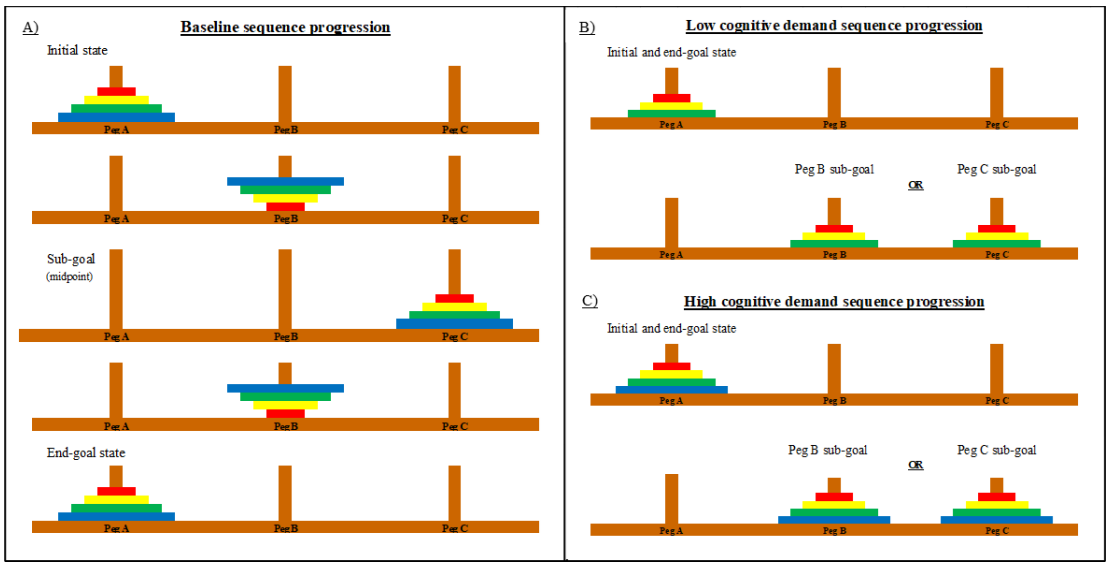

Figure 3: Sequence progression for the Baseline (BS) conditions (Panel A) and the low (Panel B) and high (Panel C) cognitive demand conditions. BS trials all had the same sub-goal and required a minimum of 16 moves. The cognitive demand trials involved a sub-goal (reach Peg B or Peg C) which was switched after each trial. The minimum number of moves required was 14 and 30 for the low and high demand conditions, respectively.

Experimental platform: physical and virtual ToH systems

In order to manipulate the relationship between the low- and high-level processes, the ToH was executed physically using a traditional, wooden ToH and

virtually using a simple, point-and-click virtual system (Figure 4). The former allows sequence execution with ‘natural’ coupling between high- and low-level processes whereas the latter preserves the high-level planning while simultaneously altering the low-level processing required to manipulate the ToH. Thus, for the low and high cognitive demand conditions, individuals performed under normal and altered sensorimotor processing conditions using the physical and virtual systems, respectively (Figure 4). The physical ToH platform was composed of three, evenly spaced pegs and 3-4 wooden disks. To manipulate this physical puzzle, individuals had to engage fine motor control of the digits to grasp the various sized disks and successfully place them onto the pegs. The virtual system used for the altered sensorimotor processing conditions was a custom-made platform (Virtualized Learning, VLEARN) modeled after the aforementioned physical system. VLEARN was developed and validated by our team in collaboration with the Department of computer science at UMD with both systems achieving usability scores significantly above industry standard (Shaver et al., 2022). VLEARN utilizes simple point-and-click controls which ultimately simplify the coordination patterns needed to manipulate the ToH components relative to its physical counterpart. More specifically, virtual disks are picked up with the left-click of a computer mouse and are released/dropped using another left-click of the mouse. In order to standardize task execution and to mitigate fatigue, a computer mouse was always used instead of a trackpad (Shaver et al., 2023). Additionally, only the dominant hand (i.e., right hand) was used for puzzle manipulation while the non-dominant hand stabilized the physical puzzle/laptop.

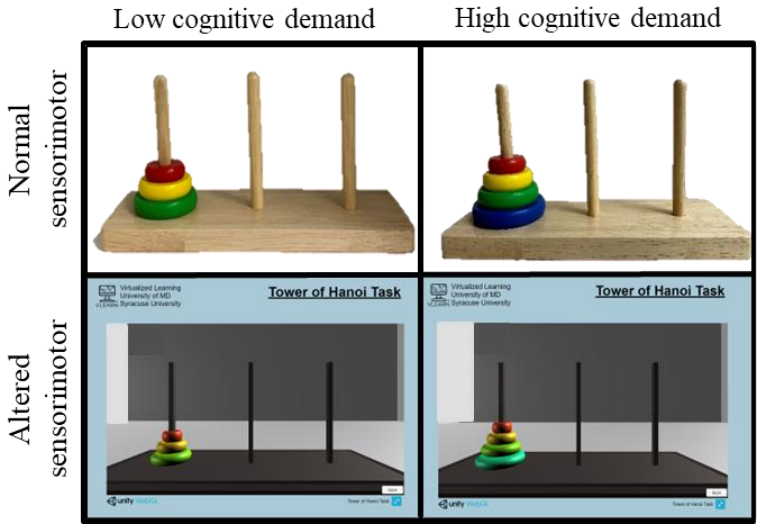

Figure 4: The low (left; 3 disks) and high (right; 4 disks) cognitive demand conditions for both the physical (top row) and virtual (bottom row) Tower of Hanoi systems used for the normal and altered sensorimotor conditions, respectively. The physical, wooden system was manipulated using the dominant right hand. The virtual system used was modeled after the physical system and employs simple point-and-click computer-mouse controls to manipulate the puzzle components (VLEARN; Shaver et al., 2022).

Protocol

Participants completed two sessions in total. During Session 1, participants provided informed consent and completed demographics questionnaires (See Participant section above). Participants were encouraged to take as much time as they needed, ask questions at any time, and were reminded that they could stop at any point without penalty. Requirements regarding abstaining from substance use 24 hours before participation were explained and participants were asked to come to Session 2 well rested with dry hair. Finally, their head size was measured in order to ensure the proper electroencephalography (EEG) cap was used during Session 2 and Session 2 was scheduled.

Upon arriving for Session 2, participants confirmed no substances that may impact the central nervous system had been ingested within 24 hours of participation

and the EEG cap was prepared. Once the EEG cap was properly placed and gelled, baseline EEG data were collected for 1 minute while participants sat quietly with their eyes open and again for 1 minute while they sat quietly with their eyes closed. Next, the chair height was adjusted based on the participant's comfort. Then participants completed a 1-minute familiarization phase during which they were allowed to manipulate the ToH system they were going to use first and make any necessary adjustments required to easily reach/manipulate the puzzle. This approach was taken to allow participants to become comfortable manipulating the puzzle components and using the simple VLEARN controls. After the first familiarization phase, participants completed a baseline condition which began with a video demonstration of an intentionally obvious and easy action sequence with 16 moves (N = 16). Then, participants were asked to imitate the sequence previously shown in the video as closely as possible and repeat it for the duration of the 3-minute trial. The inclusion of this baseline condition aimed to examine how the sensorimotor mapping affected the cerebral cortical dynamics when individuals executed the task with no cognitive task demand. To further minimize cognitive demand during this baseline sequence, the sub-goal was not switched, each trial began with a video demonstration of the intentionally simple action sequence, and participants could ask for the next move at any time.

Once the baseline sequence condition was completed using the current system, the objectives and rules for their first cognitive demand condition (low or high) were explained and both cognitive demand conditions were completed under that sensorimotor condition (normal or altered). This was repeated for the remaining sensorimotor demand condition (Figure 5). Continuous EEG and video data were

recorded for the duration of each 3-minute trial. Additionally, participants were asked to complete post-trial surveys after each 3-minute trial. Specifically, pen-and-paper versions of the NASA task load index (TLX) and was employed to assess the perceived mental workload. Visual analog scales were also used to assess fatigue but not discussed in the rest of the document since they were more exploratory in nature. The order of the two sensorimotor conditions, cognitive demand conditions, and initial sub-goal (Peg B or C; Figure 3) was counterbalanced across participants.

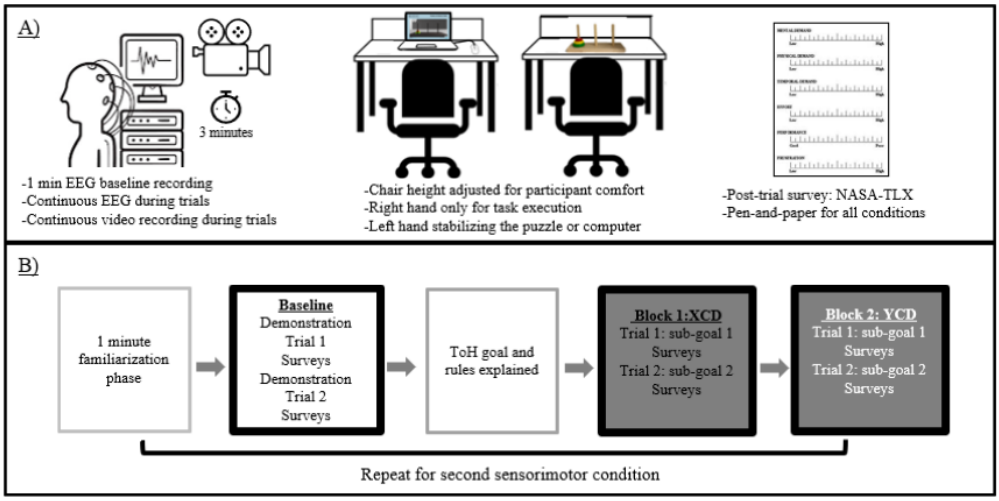

Figure 5: Panel A: Data collection components including EEG and video recordings of each 3-minute trial (left), the sensorimotor conditions (middle), and the pen-and-paper NASA-TLX (subjective mental workload). Panel B: Progression through a sensorimotor demand condition including baseline, the initial cognitive demand condition (XCD; black font), and the remaining cognitive demand condition (YCD; white font) which was repeated for the second sensorimotor demand condition. Sensorimotor, cognitive demand, and subgoal order were counterbalanced.

Data collection and processing

Performance

In order to examine different aspects of cognitive-motor performance, videos and VLEARN logs of both trials of each cognitive demand and sensorimotor demand condition were recorded. In order to emphasize cognitive-motor performance and

mitigate the practice effects, only data from the first trial of each condition was considered in the main statistical analyses. The number of puzzles completed was noted by the researcher during data collection and confirmed by rewatching trial videos. A puzzle was considered 'complete' if the participant reached the correct sub-goal followed by the end-goal within the 3-minute time-limit. Puzzles were considered 'successful' if this was accomplished without committing a rule break. If a rule break was committed and not immediately self-corrected, participants were instructed to move the involved disk back to its previous peg and continue their action sequence from that point. Puzzles with rule breaks were noted as 'unsuccessful' but still included in analyses. Instances where physical disks were dropped were noted as drops and trials were still included in analyses. If the dropped disk was within reach of the participant, they were allowed to pick it up and continue. If not, the trial was stopped and restarted. Similarly, during the altered sensorimotor conditions, participants sometimes prematurely clicked the mouse, 'dropping' the disk and unintentionally placing said disk on an unintended peg. These instances were also noted as drops and included in analyses. When a virtual drop resulted in a rule break (i.e., a larger disk being stacked on a smaller disk), they were also noted as accidental rule break. In both instances, participants could pick up the disk from the unintended peg and continue. The number of puzzles completed was determined for each trial and averaged across conditions before statistical analysis. The sequence completion time (SCT) is defined here as the time between the initiation of the first move through the completion of the last move of a ToH puzzle (i.e., time between movement initiation and reaching the end-goal after the assigned sub-goal; see Figure 3). For a more refined analysis, the SCT was divided

into cognitive (SCTc) and motor (SCTm) components. SCTc is similar to the 'pause' times described in previous work (Spitz et al., 1985; Welsh et al., 1995; M. C. Welsh, 1991; Welsh & Huizinga, 2005) whereas SCTm represents the time spent actually manipulating the task components (i.e., moving the disks from peg to peg). Therefore, SCTc and SCTm represent the portion of time individuals pause with no movement occurring (e.g., planning) and the time spent in motion during sequence execution, respectively. Using video analysis and timestamps logged by VLEARN, both SCT types were determined for each completed puzzle and averaged for each trial and then condition before statistical analysis. Instances of rule breaks were on average very limited except for the three individuals who were excluded from the subsequent analyses (see Participants section).

Although the number of puzzles completed, SCTc and SCTm are informative, they provide limited information about the structural quality of the sequences used to complete a ToH puzzle (Hauge et al., 2019, 2021; Katz et al., 2017; Shaver et al., 2023). Therefore, the structure of the executed sequences was assessed by determining the Levenshtein Distance of each completed puzzle using the Wagner-Fischer algorithm (Levenshtein, 1966; Wagner & Fischer, 1974). Levenshtein distance is a single value that represents the number of alterations that would be required to transform the action sequences performed by participants into the 'optimal' sequence (i.e., reference sequence; shortest possible sequence). More specifically, Levenshtein distance incorporates the number of extra moves inserted into the sequence (i.e., number of insertions), the number of moves omitted or 'deleted' moves (i.e., number of deletions), and the number of substituted moves (i.e., number of substitutions) in the performed

sequences compared to the optimal reference sequence. To accomplish this, an alphabet of all potential ToH actions was employed and all actions executed by participants were identified for each trial (Hauge et al., 2019, 2021; Katz et al., 2017; Shaver et al., 2023). Then, Levenshtein distance was averaged for the puzzles completed during the first trial for each participant and each condition before statistical analysis.

Perceived mental workload

After each trial, participants completed pen-and-paper post-trial surveys to evaluate subjective levels of mental workload. The NASA Task Load Index (TLX) was employed here as it is well-established and the most common method for measuring subjective mental workload (Hart, 2006; Longo et al., 2022). The TLX includes six subscales that are scored from 0-100 in increments of 5: mental demand, physical demand, temporal demand, perceived performance, effort, and frustration. Although participants provided scores for all six subscales, the mental demand dimension is of primary interest here since it is likely the most relevant to mental workload (Akizuki & Ohashi, 2015; Shaw et al., 2018a; Shuggi et al., 2019). Only the scores for the mental and physical demand subscales of the TLX were averaged across conditions, subjected to statistical analysis and reported here.

Electroencephalography

Once collected, EEG data were digitally filtered using a Kaiser window-based FIR filter including forward-backward filtering to ensure zero phase shift. The passband and stopband edge frequencies were set to 1 and 30 Hz and 0.1 and 31 Hz, respectively. The passband ripple was set to 0.01 dB with stopband attenuation of 60

dB. Ocular artifacts were reduced using the MARA and IC label toolboxes in EEGlab. Artifacts were confirmed manually before being removed. Then, data from each trial was segmented in 1-s non-overlapping windows and baseline corrected using the mean of the pre-sweep interval. The baseline corrected data were then visually inspected, and any obvious artifacts removed and baseline drifts larger than 50 mV were discarded (Blanco et al., 2016; Sörnmo & Laguna, 2005). Finally, the remaining epochs were used to determine spectral characteristics and functional connectivity in the frequency bands of interest.

The frequency bandwidths of interest were the same for both cortical effort (i.e., spectral power) and cortico-cortical communication (functional connectivity; WPLI values). These include theta (4–7 Hz), alpha (8-13 Hz), mu (8-13 Hz particularly over the central electrodes described below), low-alpha (8–10 Hz), and high-alpha (11–13 Hz). All of these frequency bandwidth and regions of interest described below have been used to study visual attention, differences in cognitive-motor task demand, and/or mental workload (Blanco et al., 2016; Gentili et al., 2014, 2018; Krigolson et al., 2017; Longo et al., 2022; M. W. Miller et al., 2011, 2014; Rietschel et al., 2012, 2014; Shaw et al., 2018).

For spectral power, the region of interest included two electrodes each (one per hemisphere) and are as follows (Figure 6): prefrontal regions are represented by anterior frontal electrodes (AF; AF7, AF8), Frontal (F; F3, F4), Central (C; C3, C4), Temporal (T; T7, T8), Parietal (P; P3, P4), and Occipital (O; O1, O2). To determine cortical effort, spectral power in each frequency bandwidth was computed across 1-Hz bins using a fast Fourier transform and then averaged for both electrodes of each

cortical region and again for both cognitive demand and sensorimotor demand conditions. Additionally, the frontal theta / parietal alpha and frontal theta / frontal alpha power ratios were determined using the frontal (F3, F4) and parietal (P3, P4) electrodes (Shaw et. al., 2018). EEG spectral power data were naturally log-transformed to approximate normal distribution before being subjected to statistical analyses.

Functional connectivity analyses in the left hemisphere were conducted by computing the WPLI between three regions of interest (Figure 6): the dlPFC (F3), PMC (FC3), and SMC (C3). More specifically, between the left dlPFC and PMC (dlPFC-PMC), left dlPFC and SMC (dlPFC-PMC), and separately between the PMC and SMC (PMC-SMC) (Anwar et al., 2016; Le et al., 2022). Electrode F3 was chosen to represent the left dlPFC because this electrode site has been used in EEG studies with electrode placement based on the same extended 10-20 international system used here as well as in several previous neuroimaging studies including physically manipulating the dlPFC using transcranial direct current stimulation under the F3 electrode (Le et al., 2022; Nitsche et al., 2009; Radman et al., 2018; Anwar et al., 2016). In particular, the WPLI values for these three pairs of electrodes were computed across 1-Hz bins, averaged for each of the theta, alpha, low-alpha and high-alpha frequency bandwidth and each condition. WPLI was chosen to assess functional connectivity because it is particularly robust to the volume conduction problem inherent to EEG (Vinck et al., 2011). Then, the WPLI values were subjected to a Fisher z transformation to approximate normal distribution before conducting statistical analyses (Shaw et al., 2019; Vinck et al., 2011).

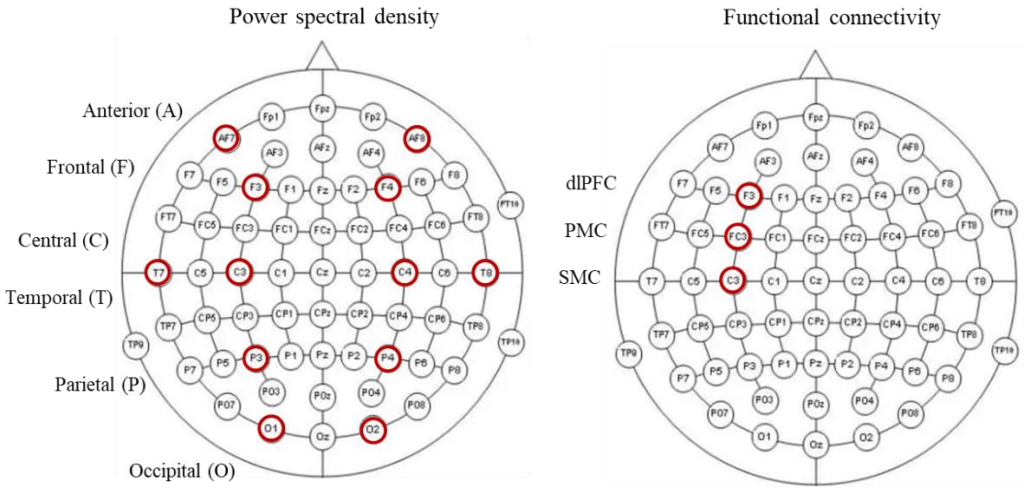

Figure 6: Electrodes representing each region of interest (ROI; red circles) for the examination of cortical effort (spectral power; left side) which include two electrodes per ROI. ROIs used in the examination of cortico-cortical communication (functional connectivity; WPLI) include one electrode from the left hemisphere per ROI.

Statistical analysis

Although all the conditions were counterbalanced, the removal of three participants (see Participants section) slightly changed the counterbalancing of the conditions. A preliminary analysis indicated that the number of puzzles completed, the SCTc, Levenshtein distance, and perceived mental demand were the only metrics impacted by the ordering of the initial condition and thus to were examined using ANCOVAS (see below).

Baseline conditions

In order to inform the main experimental part of the study (where both the cognitive demand and sensorimotor mapping were manipulated), the *baseline* measures (where only the sensorimotor map was manipulated) were also subjected to a statistical analysis. The number of puzzles completed, Levenshtein distance, and perceived mental demand observed during the *baseline* conditions were subjected to a series of

INITIAL SENSORIMOTOR [Normal first group, Altered first group] x 2 SENSORIMOTOR [Normal, Altered] ANCOVAS. The other behavioral metrics (i.e., SCT, SCTm, physical demand) as well as the EEG power and connectivity metrics were all subjected to a series of ANOVAs as described below for the main experimental conditions without the COGNITIVE DEMAND factor as the baseline conditions did not include this manipulation. The frontal theta / parietal alpha and frontal theta / frontal alpha power ratios were examined by means of paired t-tests or Wilcoxon signed-ranked tests depending on whether or not the data followed a normal distribution.

Experimental conditions

Similar to the baseline conditions, in addition to counterbalancing, order effects were examined on all of the metrics of interest. This preliminary analysis revealed that the same measures were affected by the order in which individuals experienced the sensorimotor conditions. Thus, as for the baseline, the number of puzzles completed, SCTc, Levenshtein distance, and MD measurements were subjected to a series of INITIAL SENSORIMOTOR [Normal first group, Altered first group] x 2 SENSORIMOTOR [Normal, Altered] x 2 COGNITIVE DEMAND [Low, High] ANCOVAS. The other behavioral measures such as the motor (SCTm) sequence completion times and perceived physical demand were examined by means of a series of 2 SENSORIMOTOR [Normal, Altered] x 2 COGNITIVE DEMAND [Low, High] repeated measures ANOVAs. The spectral power for each frequency bandwidth were subjected to a series of 2 SENSORIMOTOR [Normal, Altered] x 2 COGNITIVE DEMAND [Low, High] x 6 REGION [Anterior, Frontal, Central, Temporal, Parietal, and Occipital] repeated measures ANOVAs. Additionally, frontal-theta/parietal-alpha

and frontal-theta/frontal-alpha ratios were examined using separate 2 SENSORIMOTOR [Normal, Altered] x 2 COGNITIVE DEMAND [Low, High] repeated measures ANOVAs.

The WPLI values between the dlPFC and the two other regions of interest (PMC and SMC) were subjected to a 2 SENSORIMOTOR [Normal, Altered] x 2 COGNITIVE DEMAND [Low, High] x 2 REGION [SMC, PMC] repeated measures ANOVA. Finally, WPLI values between the SMC and PMC were subjected to separate 2 SENSORIMOTOR [Normal, Altered] x 2 COGNITIVE DEMAND [Low, High] repeated measures ANOVAs. For all statistical analyses, the Greenhouse-Geisser correction was employed if the sphericity assumption was violated, and p-values are reported based on the corrected degrees of freedom. Whenever needed, post-hoc analysis was conducted using the Tukey' HSD. All criterion alpha levels were $p < 0.05$.

Chapter 3: Results

Baseline conditions

Behavior: performance and subjective demand during baseline conditions

Statistical analysis of the baseline conditions revealed significant differences in behavior between the normal and altered conditions (Figure 7). In regard to performance, a main effect of SENSORIMOTOR was identified for the number of puzzles completed ($F(2, 40) = -6.38$, $p < 0.001$, $\eta_P^2 = 0.746$) and SCT ($F(2, 40) = 6.33$, $p < 0.001$, $\eta_P^2 = 0.763$). More specifically, during the altered condition, participants completed more puzzles and sequences were completed faster compared to the normal condition. However, analysis of SCTm and SCTc revealed no differences between the baseline conditions ($p > 0.050$) indicating that a similar amount of time was dedicated to movement and pause time per puzzle, respectively. Finally, Levenshtein distance was the same (Levenshtein distance = 0) during both baseline conditions indicating identical sequence structure ($p > 0.050$). Statistical analysis of the self-reported measures (i.e., NASA-TLX subscales) revealed subjective levels of mental and physical demand were impacted differently by the normal and altered conditions. Analysis of the mental demand subscale, which is thought to be most relevant to MWL assessment in a cognitive-motor context (Akizuki & Ohashi, 2015; Shaw et al., 2018a; Shuggi et al., 2019), revealed similar scores for normal and altered conditions ($p > 0.05$). However, analysis of the physical demand subscale scores revealed a main effect of SENSORIMOTOR, indicating that the physical demand was higher during the normal compared to the altered condition ($F(1, 20) = 43.959$, $p < 0.001$, $\eta_P^2 = 0.690$).

Regional Cortical activity: power spectral density during baseline conditions

Theta, low-alpha, high-alpha, and mu power as well as theta/alpha ratios were also examined (Figure 7). Statistical analysis of theta power during the baseline conditions revealed a SENSORIMOTOR x REGION interaction effect ($F(2.782, 58.419) = 9.450$, $p < 0.001$, $\eta_P^2 = 0.310$). Post hoc analysis revealed that theta power in the anterior frontal region was enhanced during the normal compared to the altered condition ($p < 0.001$, $d = 0.556$). Statistical analysis of low-alpha power during the baseline conditions revealed a SENSORIMOTOR x REGION interaction effect ($F(3.480, 73.808) = 7.335$, $p < 0.001$, $\eta_P^2 = 0.259$). Post hoc analysis revealed that low-alpha power in the anterior frontal region was enhanced during the normal compared to the altered condition ($p = 0.001$, $d = 0.789$). Statistical analysis of high-alpha power during the baseline conditions revealed a SENSORIMOTOR x REGION interaction effect ($F(3.391, 71.206) = 6.047$, $p = 0.001$, $\eta_P^2 = 0.224$). Post hoc analysis revealed that high-alpha power in the anterior frontal region was enhanced during the normal compared to the altered condition ($p < 0.050$, $d = 0.690$). Statistical analysis of mu power during the baseline conditions revealed a SENSORIMOTOR x REGION interaction effect ($F(3.557, 74.702) = 8.282$, $p < 0.001$, $\eta_P^2 = 0.283$). Post hoc analysis revealed that mu—alpha power over the central region—was reduced during the normal compared to the altered condition ($p < 0.001$, $d = 0.738$). The frontal-theta/parietal-alpha (FTPA) and frontal-theta/frontal-alpha (FTFA) ratios were also examined. Statistical analysis revealed FTPA was significantly higher in the normal compared to the altered condition ($t(21) = -2.440$, $p < 0.050$, $d = 0.606$). Similarly,

significantly higher FTFA was observed during the normal compared to the altered condition ($t(21) = 2.087$, $p < 0.050$, $d = 0.356$).

Cortico-cortical networking: functional connectivity during baseline conditions

When examining WPLI values for the left hemisphere PMC-SMC pair, significant differences in theta were revealed (Figure 7). More specifically, theta SMC-PMC connectivity was significantly enhanced during the altered compared to the normal sensorimotor condition ($t(21) = 2.551$, $p = 0.018$, $d = 0.369$). Statistical analysis of functional connectivity within the low-alpha and high-alpha bands during the baseline conditions revealed no relevant effects related to the sensorimotor conditions ($p > 0.05$).

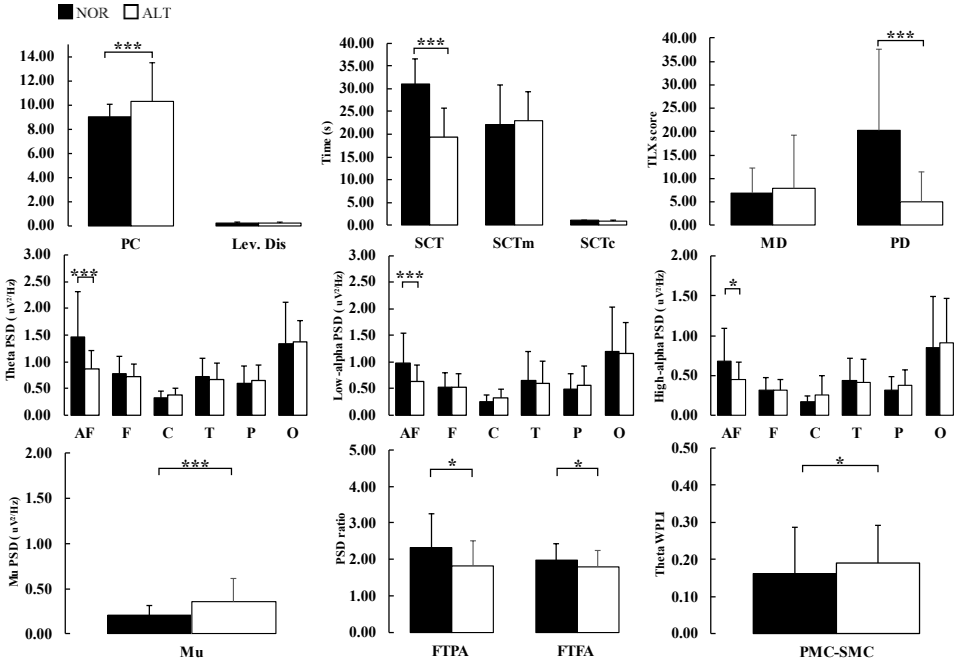

Figure 7: Results for the normal (physical system; black) and altered (virtual system; white) baseline conditions. *Top:* Average number of puzzles completed (PC), Levenshtein distance (Lev. Dis), sequence completion time (SCT) with its motor (SCTm) and cognitive (SCTc) components in seconds, and subjective mental (MD) and physical (PD) demand TLX scores. *Middle:* Power spectral density (PSD, uV^2/Hz) in the frequency bands of interest over the anterior (AF), frontal (F), central (C), temporal (T), parietal (P), and occipital (O) regions. *Bottom:* Mu PSD, frontal-

theta/parietal-alpha (FTPA) and frontal-theta/frontal-alpha (FTFA) PSD ratios, and theta functional connectivity (WPLI values) between the premotor (PMC) and sensorimotor (SMC) cortices. *p<0.050; **p<0.010; ***p<0.001.

Experimental conditions

Behavior: performance and subjective demand during experimental conditions

Statistical analysis of the experimental conditions (i.e., low and high cognitive demand under normal and altered sensorimotor conditions), revealed significant differences in behavior between the normal and altered conditions as well as between the low and high demand conditions (Figure 8). Statistical analysis of the number of puzzles completed revealed a main effect of SENSORIMOTOR ($F(1, 19) = 59.634$, $p < 0.001$, $\eta_P^2 = 0.402$) such that more puzzles were completed during the altered compared to normal conditions. Further, a main effect of COGNITIVE DEMAND was identified such that participants completed significantly more puzzles in the low relative to the high demand conditions ($F(1, 19) = 383.908$, $p < 0.001$, $\eta_P^2 = 0.954$). Analysis of SCTm revealed a main effect of SENSORIMOTOR such that participants spent less time moving disks between pegs in the normal compared to the altered conditions ($F(1, 19) = 50.817$, $p < 0.001$, $\eta_P^2 = 0.296$). The same analysis revealed a main effect of COGNITIVE DEMAND on SCTm, indicating that participants spent less time moving the disks in the high relative to the low demand conditions ($F(1, 19) = 705.366$, $p < 0.001$, $\eta_P^2 = 0.952$). Statistical analysis of SCTc revealed a main effect of SENSORIMOTOR such that participants spent more time paused when completing puzzles during the normal compared to the altered conditions ($F(1, 19) = 8.047$, $p < 0.001$, $\eta_P^2 = 0.190$). In addition, the examination of SCTc revealed a main effect of

COGNITIVE DEMAND such that participants spent more time paused completing the puzzles in the high relative to the low demand ($F(1, 19) = 89.400$, $p < 0.001$, $\eta_P^2 = 0.830$). Therefore, in the normal vs. altered and high vs low demand conditions, significantly less movement time (i.e., SCTm) was accompanied by significantly more pause time (i.e., SCTc). For Levenshtein distance, only a main effect COGNITIVE DEMAND was observed and indicated significantly lower Levenshtein distance (i.e., better sequence structure) during the low relative to the high demand conditions ($F(1, 19) = 141.051$, $p < 0.001$, $\eta_P^2 = 0.888$). Statistical analysis of the self-reported measures (i.e., NASA-TLX subscales) revealed subjective levels of mental and physical demand were impacted differently by the sensorimotor and cognitive demand manipulations. More specifically, statistical analysis of the mental demand subscale scores revealed a main effect of COGNITIVE DEMAND which indicated that perceived mental demand was higher in the high compared to the low cognitive demand conditions ($F(1, 20) = 61.754$, $p < 0.001$, $\eta_P^2 = 0.726$). Analysis of the physical demand subscale scores revealed a main effect of SENSORIMOTOR such that perceived physical demand was higher during the normal compared to the altered conditions ($F(1, 21) = 9.508$, $p < 0.001$, $\eta_P^2 = 0.310$).

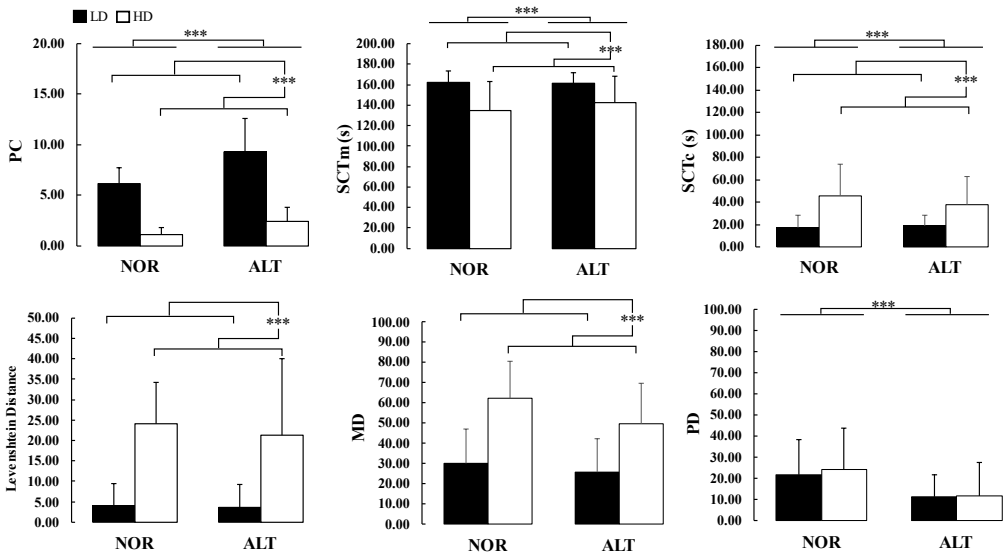

Figure 8: The average number of puzzles completed (PC), motor (SCTm) and cognitive(SCTc) sequence completion times in seconds, Levenshtein distance, subjective mental (MD) and physical (PD) demand scores for the normal (NOR; physical system) and altered (ALT; virtual system) sensorimotor conditions during the low (LD; black) and high (HD; white) cognitive demand conditions. *p<0.050; **p<0.010; ***p<0.001.

Regional Cortical Activity: power spectral density during experimental conditions

Theta, low-alpha, high-alpha, and mu power as well as theta/alpha power ratios were considered in order to characterize the neural engagement patterns that support complex action sequence execution under normal and altered sensorimotor conditions in the presence of low and high cognitive demand. Statistical analysis of theta power during the experimental conditions revealed a SENSORIMOTOR x REGION interaction effect ($F(2.886, 57.721) = 14.432$, $p < 0.001$, $\eta_P^2 = 0.419$). Post hoc analysis revealed that theta power was enhanced over the anterior frontal ($p < 0.001$, $d = 0.820$), temporal ($p < 0.001$, $d = 0.560$), and occipital ($p < 0.050$, $d = 0.410$) regions during the normal compared to the altered conditions. An interaction effect between COGNITIVE DEMAND x REGION was also detected for theta power ($F(2.610, 52.306) = 2.983$, $p < 0.050$, $\eta_P^2 = 0.130$). Post-hoc analysis revealed enhanced theta power in the anterior

frontal ($p < 0.001$, $d = 0.300$), frontal ($p < 0.050$, $d = 0.340$), and occipital ($p < 0.050$, $d = 0.380$) regions during the high cognitive demand conditions compared to the low cognitive demand conditions (Figure 9).

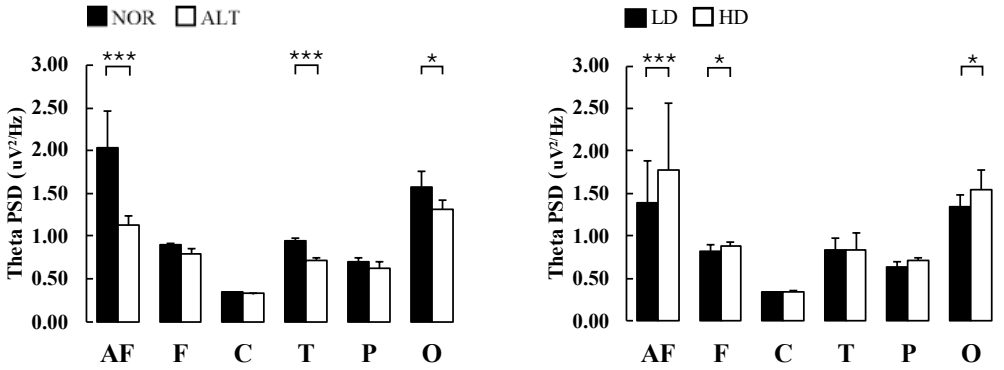

Figure 9: Theta power spectral density (PSD, uV^2/Hz) over the anterior (AF), frontal (F), central (C), temporal (T), parietal (P), and occipital (O) regions of interest observed during the normal (NOR; physical system) and altered (ALT; virtual system) sensorimotor conditions (left) and during the low (LD) and high (HD) cognitive demand conditions (right). *p<0.050; **p<0.010; ***p<0.001.

Similar to theta, statistical analysis of low-alpha power during the experimental conditions revealed a SENSORIMOTOR x REGION interaction effect ($F(3.219, 64.385) = 14.571$, $p < 0.001$, $\eta_P^2 = 0.421$). Post hoc analysis revealed enhanced low-alpha power over the anterior frontal ($p < 0.001$, $d = 0.970$), temporal ($p < 0.001$, $d = 0.400$), and occipital ($p < 0.001$, $d = 0.440$) regions during the normal compared to altered conditions. Additionally, a COGNITIVE DEMAND x REGION interaction effect was identified for low-alpha ($F(3.320, 66.391) = 3.375$, $p < 0.050$, $\eta_P^2 = 0.114$). However, post hoc analysis revealed no significant effects (Figure 10). In regard to high-alpha power, analysis of the experimental conditions indicated a SENSORIMOTOR x REGION interaction effect ($F(3.244, 64.870) = 11.976$, $p < 0.001$, $\eta_P^2 = 0.375$). Post hoc analysis revealed enhanced high-alpha power over the anterior frontal ($p < 0.001$, $d = 0.710$) and occipital ($p < 0.010$, $d = 0.410$) regions

during the normal relative to the altered condition. Also, a SENSORIMOTOR x REGION ($F(3.401, 68.019) = 16.343$, $p < 0.001$, $\eta_P^2 = 0.283$) interaction effect was revealed and indicated mu was reduced during the normal conditions compared to the altered ($p < 0.050$, $d = -0.738$) (Figure 10).

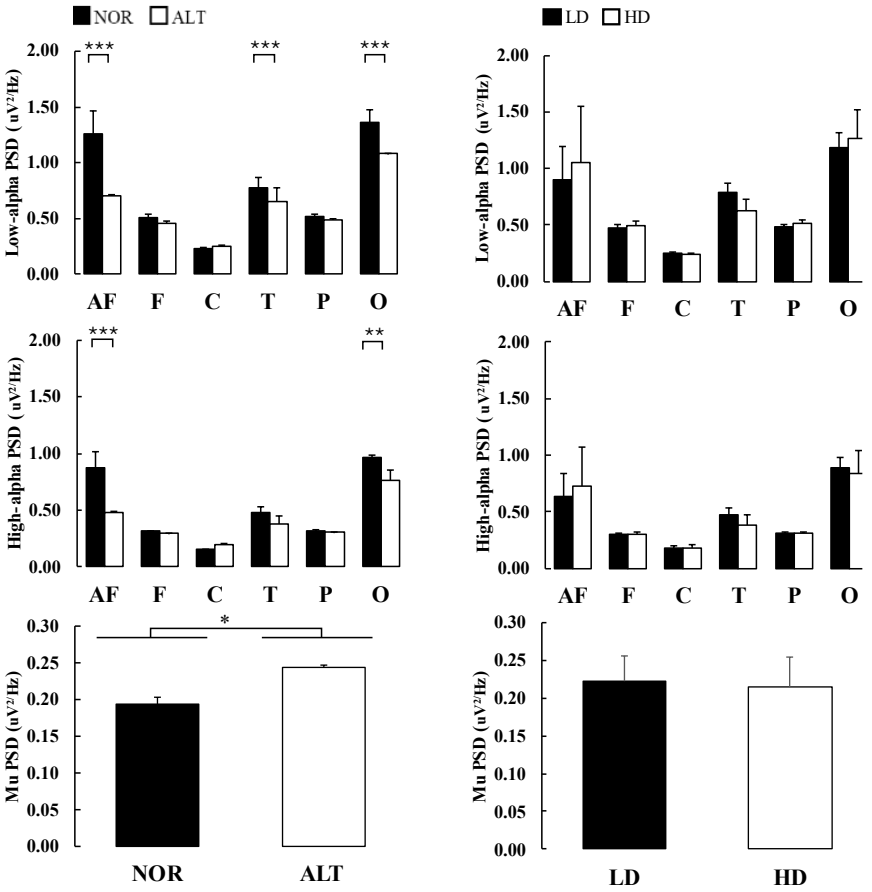

Figure 10: Power spectral density (PSD, uV^2/Hz) in the low-alpha (top), high-alpha (middle), and mu (bottom) frequency bands over the anterior (AF), frontal (F), central (C), temporal (T), parietal (P), and occipital (O) regions of interest observed during the normal (NOR; physical system) and altered (ALT; virtual system) sensorimotor conditions during the low (LD) and high (HD) cognitive demand conditions. *p<0.050; **p<0.010; ***p<0.001.

Theta/alpha ratios for the experimental conditions were also evaluated (Figure 11). Analysis of the frontal-theta/parietal-alpha power ratio did not reveal any significant main or interaction effects. The same analysis for the frontal-theta/frontal-alpha ratios revealed a main effect of COGNITIVE DEMAND ($F(1, 20) = 8.842$, $p <$

0.010, η_P^2 =0.307) such that the frontal-theta/frontal-alpha power ratio was larger during the high relative to the low demand conditions.

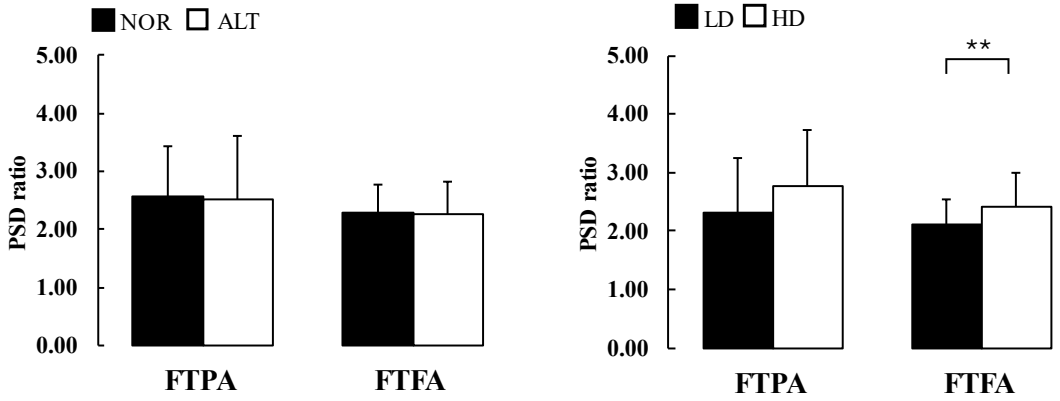

Figure 11: Frontal-theta/parietal-alpha (FTPA) and frontal-theta/frontal-alpha (FTPA) power spectral density (PSD, uV^2/Hz) ratios observed during the normal (NOR; physical system) and altered (ALT; virtual system) conditions (left) and the low (LD) and high (HD) cognitive demand conditions (right). *p<0.050; **p<0.010; ***p<0.001

Cortico-cortical networking: functional connectivity during experimental conditions

Communication between the left dlPFC and the left PMC (dlPFC-PMC) and left SMC (dlPFC-SMC) as well as between the left PMC and left SMC (PMC-SMC) were examined for the experimental conditions in the theta, low-alpha, and high-alpha bands. When WPLI values of the dlPFC-PMC and dlPFC-SMC pairs in the theta band were subjected to statistical analysis, a significant REGION x COGNITIVE DEMAND interaction effect was detected ($F(1, 20) = 13.534$, $p = 0.001$, η_P^2 =0.404). Post hoc testing revealed that the dlPFC-PMC connectivity was greater compared to dlPFC-SMC connectivity during both the (i) low ($p < 0.001$, $d = 1.35$) and (ii) high ($p < 0.001$, $d = 1.59$) demand conditions. Post hoc analysis also revealed that both (iii) dlPFC-PMC ($p < 0.001$, $d = 0.424$) and (iv) dlPFC-SMC ($p = 0.007$, $d = 0.357$) connectivity increased with cognitive demand. An interaction effect between SENSORIMOTOR x

COGNITIVE DEMAND ($F(1, 20) = 4.525$, $p < 0.050$, $\eta_P^2 = 0.184$) was also revealed. Post hoc analysis indicated that the combined dlPFC-PMC and dlPFC-SMC theta connectivity significantly increased from low to high cognitive demand during the normal sensorimotor condition (v) ($p < 0.010$, $d = 0.440$) whereas this was not observed in the altered conditions ($p = 0.667$, $d = 0.173$).

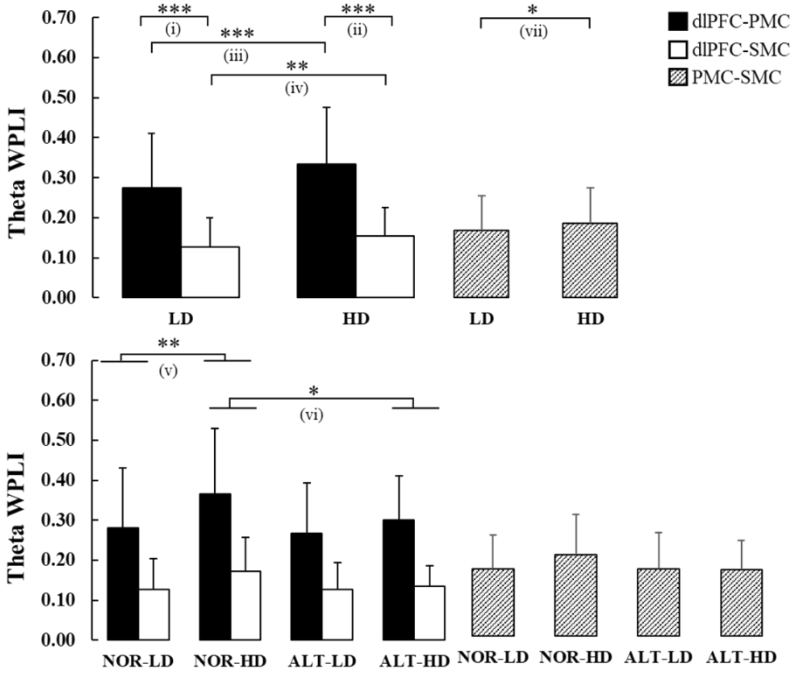

Figure 12: Differences in theta functional connectivity between the left dorsolateral prefrontal cortex (dlPFC) and the left premotor cortex (dlPFC-PMC), left sensorimotor cortex (dlPFC-SMC), as well as between the left PMC and left SMC (PMC-SMC) for the low (LD) and high (HD) cognitive demand conditions and the normal (NOR) and altered (ALT) sensorimotor conditions. *p<0.050; **p<0.010; ***p<0.001.

Also, under high demand, the combined dlPFC-PMC and dlPFC-SMC connectivity was greater during the normal sensorimotor compared to the altered condition (vi) ($p = 0.021$, $d = 0.358$) whereas this was not observed during the low demand ($p = 0.997$, $d = 0.053$). When WPLI values for the PMC-SMC pair within theta were compared between the experimental conditions, only an effect of COGNITIVE DEMAND (vii) ($F(1, 20) = 4.656$, $p < 0.050$, $\eta_P^2 = 0.189$) was identified and indicated

that an increase in cognitive demand prompted enhanced (vii) PMC-SMC connectivity (Figure 12). Statistical analysis also revealed an interaction effect between SENSORIMOTOR x COGNITIVE DEMAND for low-alpha ($F(1, 20) = 4.922$, $p < 0.050$, $\eta_P^2 = 0.197$) and high-alpha ($F(1, 20) = 8.472$, $p < 0.010$, $\eta_P^2 = 0.298$). However, post hoc testing could not identify the locus of either of these interactions ($p > 0.05$). When the PMC-SMC functional connectivity during the experimental conditions within the low-alpha and high-alpha bands were subjected to statistical analysis a SENSORIMOTOR x COGNITIVE DEMAND interaction effect was observed for low-alpha ($F(1, 20) = 5.378$, $p < 0.05$, $\eta_P^2 = 0.212$) and high-alpha ($F(1, 20) = 5.360$, $p < 0.050$, $\eta_P^2 = 0.211$).

Chapter 4: Discussion

It was hypothesized that if altering the sensorimotor conditions using a simple virtual system to perform complex action sequences benefits the relationship between high- and low-level processes, these altered sensorimotor conditions would result in better performance and lower regional cortical effort compared to normal sensorimotor conditions (i.e., using a physical system). Further, if this alteration is indeed beneficial, more efficient cortico-cortical networking was expected as indicated by more efficient functional connectivity along with lower subjective mental workload. However, if this alteration misaligns or perturbs the high- and low-level relationship, the opposite was predicted. Regardless, these differences were expected to be more pronounced in the high but not necessarily the low cognitive demand conditions. Also, greater mental workload was expected as cognitive demand increased regardless of the sensorimotor condition. The discussion below is organized as follows. In the main first part, the results from the baseline are discussed (starting with the behavior, followed by regional cortical activity and then the cortico-cortical networking). In the second part, findings from the study combining both sensorimotor and cognitive demand manipulations are discussed. In this second part, the results related to the sensorimotor and cognitive demand manipulations are discussed first and second, respectively.

Baseline conditions: sensorimotor manipulation under minimal cognitive demand

Behavior and regional cortical activity under minimal cognitive demand

In the present work, participants first completed a baseline condition that involved executing a simple action sequence which imposed minimal cognitive demand under normal and altered sensorimotor conditions. During this largely motor task, participants completed fewer sequences, required more time per sequence, and reported significantly higher physical demand during the normal compared to the altered conditions. These differences may be due to the fact that under normal conditions individuals had to use complex fine motor coordination to physically manipulate the ToH disks whereas the simple point-and-click virtual system controls were easier to implement (Ceja et al., 2018; Wong et al., 2015) resulting in faster puzzle completion and lower perceived physical demand.

The theta power was modulated in the anterior frontal regions such that it was greater for the normal compared to the altered condition. Since theta band fluctuations were suggested to reflect the recruitment of attentional resources for working memory, action/error monitoring, concentration in cognitive and motor tasks, it is possible that task execution under the normal modality, prompted further recruitment of cognitive-motor resources for the fine motor coordination needed to physically manipulate the ToH disks compared to the virtual task execution which used a simpler sensorimotor mapping (Coombes et al., 2005; Gentili et al., 2011, 2014; Gevins & Smith, 2000, 2003; Hsieh & Ranganath, 2014; Jaiswal et al., 2010; Keller et al., 2017; M. W. Miller et al., 2014; Miyata, 1990b; Slobounov et al., 2000; Wong et al., 2015). The increase in theta power over the anterior frontal sites observed here is consistent with evidence of the

region's role in error monitoring and movement kinematics which are key to successful displacement in general and especially when more complex movements are executed (Cavanagh et al., 2009; Gentili et al., 2011; Larson & Lynch, 1989; Yordanova et al., 2004). This also agrees with previous work that observed increased anterior frontal effort during tasks which engaged attention in a structured manner (Liu et al., 2018). Further, excessive theta has been associated with poor performance, increased effort and fatigue which is coherent with increased physical demand as observed here (Cao et al., 2014; Talukdar et al., 2019). This is also in agreement with a prior fNIRS study which revealed that compared to the virtual execution of the ToH, the physical completion of this task led to an elevation of the dlPFC activity (Ceja, 2019; Ceja et al., 2018; Milla et al., 2019). The notion that the normal condition would impose a greater sensorimotor demand on the motor system compared to the altered condition is also in agreement with the attenuation of mu-rhythm in the central regions indicating less cortical activity from the SMC and the primary motor area during task execution for the latter compared to the former (Brunsdon et al., 2020; Cannon et al., 2014; Orgs et al., 2008; Pfurtscheller, 1992). This idea is further supported by the theta/alpha ratios (FTPA and FTFA) which are well-known metrics indexing mental workload. Specifically, the greater power ratios during the baseline conditions suggest increased mental workload during the normal compared to the altered condition (e.g., Pruziner et al., 2019; Shaw et al., 2018).

In addition, greater anterior frontal low-alpha and high-alpha power were observed during normal compared to altered performance. Such an increase of low-alpha (~8-10 Hz) and high-alpha (~11-14 Hz) have been suggested to reflect a decrease

of general arousal and reduced recruitment of task-specific resources, respectively (Klimesch, 1999, 2012; Klimesch et al., 2007; Shaw et al., 2018, 2019). This was unexpected as enhanced alpha power is generally associated with decreases in cognitive-motor effort and enhanced performance which does not seem to be the case for the normal condition given the performance, survey, theta power, mu-rhythm, and theta/alpha ratio results. In this context, alpha-band activity would rather reflect inhibition of information related to the environment. Thus, such an increase of alpha power would indicate stronger inhibition or less engagement of irrelevant resources during task performance (Klimesch, 1999, 2012; Klimesch et al., 2007). In particular, it has been suggested that activity in the alpha band may help emphasize task-relevant information by actively suppressing irrelevant sensory inputs (Foxe & Snyder, 2011; Gray et al., 2015; Robinson et al., 2024) or competing relational mappings (Benedek et al., 2014). This is also in line with previous research that observed increased alpha during tasks when distractions were more likely to interfere (Liu et al., 2018). From an anatomical standpoint, this is also supported by the role of the anterior frontal region in continuously updating and evaluating incoming sensory information, the representation of relationships between stimuli, reward, and guiding response selection and suppression (Gentili et al., 2011, 2013; Ramnani & Owen, 2004). Therefore, given the performance and subjective demand results, it is likely that physical task execution required greater engagement of inhibition since, compared to the virtual system, execution using the physical system involved a much denser set of stimuli from the environment (e.g., physics of the objects to manipulate; 3D vision processing; richer sensory feedback; more complex fine motor coordination). Thus, relative to virtual

execution, physical performance resulted in the need to increase the inhibition of i) irrelevant sensory inputs and distractors resulting in a decreased general arousal as indexed by an elevation low-alpha power as well as ii) irrelevant task-specific processing resources as indicated by an increase of high-alpha power over the anterior frontal region.

Therefore, altogether, these results indicate that compared to the virtual execution, the physical completion of the task which required more complex fine sensorimotor manipulations of the disks led in slightly degraded performance and higher perceived physical demand along with a greater need to deploy working memory, attention and action monitoring as well as a greater inhibition of the sensory stimuli generated by a richer physical space and feedback from more complex motion.

Behavior and cortico-cortical communication under minimal cognitive demand

The only relevant significant difference in functional connectivity affected by the sensorimotor manipulation during the baseline conditions was an increase of PMC-SMC connectivity in the theta band during the altered condition compared to the normal condition. Two potential competitive mechanisms could be considered here. First, in the altered condition individuals could have engaged a sensorimotor mapping which could be considered somewhat unnatural to manipulate the disks compared to that used in the physical environment. As such, this sensorimotor mapping would require greater connectivity between the PMC and SMC. This would agree with the notion that increased PMC-SMC connectivity in theta band serves as a mechanism to cope with increasing motor demand (Caplan et al., 2003; Cruikshank et al., 2012; Huang & Sereno, 2018; Van Hoornweder et al., 2022). This would suggest that enhanced

performance during virtual relative to physical execution comes at a greater PMC-SMC connectivity cost, indicated by a greater cortico-cortical communication. While possible, the notion of higher cost during the virtual conditions would somewhat contradict the smaller perceived physical demand reported for the virtual compared to physical conditions. Instead, another possible mechanism could be that, compared to physical execution, the altered execution offered simplified sensorimotor mapping, would have facilitated movement itself by increasing the motor output. Greater motor output would have been enabled through a greater exchange of information via enhanced PMC-SMC theta connectivity. Ultimately, this would have resulted in better sensorimotor performance (Vecchio et al., 2022) indicated by completing faster puzzle while also reducing the perceived physical demand during the altered baseline condition (Abe & Hanakawa, 2009; Alahmadi, 2024; Hassan et al., 2014). Thus, this increased PMC-SMC theta connectivity could be related to the increased motor output (i.e., speed, number of puzzles completed) during the altered condition which is consistent with the notion that enhanced theta connectivity is associated with better performance in young and older individuals during simple to increasingly complex upper limb movements (Rosjat et al., 2018; Van Hoornweder et al., 2022). This also agrees with previous neuroimaging studies showing that bi-directional effective connectivity (Anwar et al., 2016; Bajaj et al., 2014; Rehme et al., 2013) and functional connectivity (Bestmann et al., 2008) between the SMC and PMC is critical for performance of motor tasks involving the hand. In particular, previous work regarding the close relationship of the PMC influencing the SMC has revealed that their communication is directly supported by their anatomical connections (Alahmadi, 2024;

Hassan et al., 2014) suggesting further engagement of both regions is critical to greater motor performance as it is the case during the baseline condition as this task was essentially motor (Abe & Hanakawa, 2009). This is also in agreement with a large body of work implicating PMC in motor planning and the SMC in voluntary movement execution (Anwar et al., 2013, 2016a; Lutz et al., 2000; Zhang et al., 2010). Thus, compared to physical execution, the enhanced PMC-SMC theta connectivity may have reflected a greater engagement of motor planning processes leading to enhanced motor performance during the altered baseline condition.

Experimental conditions: manipulations of both sensorimotor and cognitive demands

Behavior related to sensorimotor conditions

Comparisons of the altered conditions to the normal conditions revealed that while the execution of the sequence structures was similar (i.e., comparable Levenshtein distance), the physical conditions with normal sensorimotor mapping produced a decline in performance outcomes (fewer PC, longer SCTc, and less SCTm) along with greater perceived physical demand. These findings suggest that individuals may have prioritized the quality of the sequence structure to be generated (i.e., high-level planning) by pausing more often to the detriment of velocity at which the task was completed during the normal relative to altered conditions. Thus, it is plausible that an increase of the amount of time spent on planning (i.e., SCTc) during the normal experimental conditions was a compensation strategy for facing cognitive task demand combined with a more demanding fine motor coordination, ultimately affording similar

sequence structure as those obtained in the altered experimental conditions which involve simple point-and-click controls (Fitts & Posner, 1967; Wong et al., 2015). This pattern of behavior may suggest that, to some extent, the more demanding fine motor control used in the normal condition would need to recruit cognitive resources that are also shared for task sequencing (e.g., attention, inhibition, working memory) compared to the altered condition. Such resource sharing would result in increased pause time (i.e., increased of SCTc) as a compensation strategy when time-sharing cognitive and motor resources is not possible or challenging (Kahneman, 1973; Wickens, 2002; Wickenst & Llu, 1988). This compensation strategy, which is in line with the classical speed-accuracy trade-off (Fitts & Posner, 1967), would prioritize task sequencing while limiting an excessive elevation of the mental workload at the cost of decreasing task execution speed resulting not only in similar sequence structure but also in comparable FTPA, FTFA ratios, and NASA-TLX MD scores.

Regional cortical activity related to sensorimotor conditions

Differences between the normal and altered conditions also led to changes in regional cortical activity regardless of the cognitive demands. Namely, similarly to the baseline, the normal condition revealed greater theta, low-alpha, and high-alpha power for the anterior frontal region along with an attenuation of central mu-rhythm when compared to the altered condition for both cognitive demand conditions. However, the mere presence of cognitive demand modulations led to significant differences in theta, low-alpha, and high-alpha power in the occipital regions along with a larger theta and low-alpha power in the temporal region during the normal compared to altered

experimental conditions - patterns not present in the normal compared to the altered baseline conditions.

Anterior and central regional cortical activity

The findings revealed that, the cortical dynamics modulations of the anterior frontal and central regions related to sensorimotor mapping modulations were common to minimally cognitively demanding conditions (i.e., baseline) and with variations in cognitive demand (i.e., low and high demand conditions). Therefore, the neurocognitive processes underlying these cortical dynamics were likely specific to the modality of execution (i.e., normal vs. altered) and somewhat independent of the presence of the cognitive demand. As discussed earlier, the theta and alpha modulations in the anterior frontal region would reflect a greater engagement of action monitoring and a greater inhibition of irrelevant stimuli during the normal condition which engages more demanding 3D action-perception processes compared to the altered condition. This is consistent with the idea that the anterior frontal region would be responsible for continuously updating and evaluating incoming sensory information, the representation of relationships between stimuli, response suppression, error monitoring and movement kinematics (Cavanagh et al., 2009, 2012; Gentili et al., 2011; Larson & Lynch, 1989; Ramnani & Owen, 2004; Yordanova et al., 2004). In addition, as previously discussed the attenuated mu-rhythm also supports the notion that more demanding fine motor control in 3D execution would further engage the sensorimotor cortex in the normal compared to the altered condition where only limited computer mouse motion were needed for task completion (Brunsdon et al., 2020; Cannon et al., 2014; Orgs et al., 2008; Pfurtscheller, 1992).

Temporal and occipital regional cortical activity

The different sensorimotor mapping induced modifications in temporal and occipital cortical dynamics which could be explained by the specific role of each of these regions. First, the involvement of theta oscillations of temporal cortices in forming associations between different sources of information is well established (Karakaş, 2020; Pitsik, 2025). In particular, enhanced temporal theta power would reflect greater working memory engagement resulting in increased mental workload (Axmacher et al., 2007, 2008; Magosso & Borra, 2024). For instance, in the context of sequential tasks, greater temporal theta power has been associated with successfully retrieval of information from working memory and the (re)activation of contextual information (Cabeza, 2012; Crespo-Garcia et al., 2010; Crespo-García et al., 2016; Hsieh & Ranganath, 2014; Mizelle & Wheaton, 2011; Sakirov, 2023). Therefore, compared to the altered condition, the normal sensorimotor mapping would provide richer contextual information requiring the need to further engage sensory integration and working memory not only to sub-serve the sensorimotor processes but also to successfully complete action sequences under different cognitive demands. Namely, in this situation the working memory will have to not only encode sensorimotor information for motion control but also to execute the action sequence. In addition, it was suggested that enhanced temporal alpha power may represent the suppression of information already encoded to facilitate acquisition of novel upcoming information (Cooper et al., 2003; Fell et al., 2011; Klimesch et al., 2007a; Min & Herrmann, 2007; Ostrowski & Rose, 2024). Therefore, while the increase of temporal theta power would indicate a greater recruitment of working memory, an enhanced low-alpha power in the

temporal region during the normal relative to altered conditions may represent inhibition of already acquired information to facilitate encoding of new information for subsequent task processing. More generally, the roles of the temporal region described above are supported by lesion and clinical population research which revealed that damage to or inactivation of the temporal region results in severe cognitive-motor impairments (Chauvière et al., 2009; Fu et al., 2018; Ge et al., 2013; Uhlhaas & Singer, 2006) and different types of apraxia (Park, 2017; Rounis & Binkofski, 2023; Rounis & Humphreys, 2015; Wheaton & Hallett, 2007).

Besides the temporal regions, greater theta, low-alpha, and high-alpha power in the occipital region was detected which would indicate a greater recruitment of visual-related processes for the normal compared to the altered sensorimotor conditions. Namely, it was suggested that theta oscillations in the occipital regions are involved in the multimodal associative processing to integrate sensory information from various modalities (Karakaş, 2020; Pitsik, 2025). Also, greater occipital theta power would represent enhanced visual information identification and processing (Cartier et al., 2012; Makarov et al., 2021). Consistent with these theta findings was the elevation of alpha power in the occipital regions which are thought to play a role in actively shaping perception, representing visual input regulation (Klimesch, 1999; Klimesch et al., 2007; Romei et al., 2010). Specifically, low-alpha enhancement has been correlated with better cognitive-motor performance and is thought to characterize the active selection of targets across spatial locations, allowing participants to respond faster by inhibiting irrelevant sensory information (Foxe & Snyder, 2011; Magosso & Borra, 2024; Vecchio et al., 2022). Thus, during the normal sensorimotor conditions, the

changes in theta and alpha power in the occipital regions would represent a greater recruitment of the processes related to multimodal sensory association and the identification of specific relevant stimulus through enhanced inhibition of visual information.

Therefore, as a whole, the anterior frontal, temporal, central, and occipital cortical dynamics suggests that, compared to the altered condition, the use of the normal sensorimotor condition mapping would provide richer information due to 3D action-perception dynamics which prompt increased action monitoring, working memory, visual processing, sensory integration, motor activation, and active inhibition to suppress irrelevant information during sensorimotor performance but also more planning time to execute the action sequence properly in the presence of cognitively demanding tasks which ultimately resulting in similar Levenshtein distance for both sensorimotor conditions. Interestingly, the results of the baseline and the subsequent study may suggest that, while the anterior frontally and centrally-mediated processes observed here may mainly be used for motion execution and regulation, the temporally and occipitally-mediated processes could be possibly involved when these sensorimotor demands are combined with the need to address cognitive demands (e.g., select the right hand shape for a given disk size based on the correct disk to be moved to the corresponding peg to correctly implement the sequence and solve the problem). Collectively, these findings suggest that regardless of the cognitive demands, the normal sensorimotor condition led to a greater recruitment of cognitive-motor resources indicating a higher level of mental workload relative to the altered condition.

Regional cortical activity related to cognitive demand conditions

As expected, the high demand conditions resulted in fewer puzzles completed, less execution (i.e., SCTm) and more planning (i.e., SCTc) time along with a degraded sequence structure (i.e., higher Levenshtein distance), and increased perceived mental demand. These behavioral results suggest that the high demand conditions increased mental workload, resulting in a decrement of high-level performance (i.e., worse sequence structure; higher Levenshtein distance). Thus, similarly to the effects induced by the change in sensorimotor mapping, the elevation of cognitive demand led to a decrease of the time spent moving the disks along with more pauses. This may suggest a similar compensation strategy as discussed earlier when comparing the normal and altered sensorimotor conditions without however being able to fully compensate for the increase of cognitive demand as indicated by impaired sequence structure performance (i.e., increased of Levenshtein distance) and an elevation of perceived mental demand. The increase of cognitive task demand also resulted in changes of cortical dynamics which were restricted to the theta power bandwidth and the FTFA power ratio. Specifically, theta power increased over the anterior frontal as well as frontal regions as cognitive demand increased. The theta power modulations in these two cortical regions are consistent with the idea that greater engagement of attention, action/error monitoring, and working memory would have been deployed when individuals had to solve more cognitively demand version of the task (Coombes et al., 2005; Gentili et al., 2011, 2014b; Gevins & Smith, 2000, 2003; Hsieh & Ranganath, 2014; Jaiswal et al., 2010; Keller et al., 2017b; M. W. Miller et al., 2014a; Miyata, 1990b; Slobounov et al., 2000). The observed frontal theta elevation agrees with a large body of work

implicating dlPFC (i.e., frontal region here; Anwar et al., 2016) engagement in response to increased demand during ToH performance (Ceja, 2019; Ceja et al., 2018a; Fabbri-Destro et al., 2009; Naylor & Briggs, 1963; Ruocco et al., 2014; Wilmut et al., 2013). Furthermore, these cortical changes were accompanied by an elevation of theta power in the occipital regions as the cognitive demand increases. Such an increase in occipital theta power would be reflective of increased deployment of visual information processing resources which are necessary for individuals to generate and complete action sequences to solve problems when cognitive demand is high (Cartier et al., 2012; Makarov et al., 2021). These frontal and occipital theta modulations are further supported by a higher FTFA power ratio obtained which indicates a greater mental workload during the high compared to the low cognitive task demand. Our results agree with those from previous studies which revealed that an elevation of the level of challenge with the ToH task resulted in higher mental workload level although these investigations employed only virtual task execution (Hardy & Wright, 2018; Radüntz, 2020). It must be noted that unlike the baseline and the contrast between sensorimotor conditions (i.e., normal vs. altered), the elevation of cognitive task demand led to similar mu power. This suggests that neural resource allocation related to movement execution task (Brunsdon et al., 2020; Cannon et al., 2014; Orgs et al., 2008; Pfurtscheller, 1992) was not directly impacted by cognitive demand in these healthy, young participants despite reduced SCTm in the high cognitive demand conditions.

Corticocortical communication

Cortico-cortical networking affected by changes of sensorimotor conditions

The results revealed that changing the sensorimotor conditions modified the functional relationships between regions such that there was an elevation of connectivity for both the dlPFC-PMC and dlPFC-SMC pairs in the theta bandwidth. Namely, the theta connectivity between the dlPFC and both the PMC and SMC increased i) as the cognitive demand was augmented under the normal but not the altered conditions and ii) in the normal relative to the altered condition only under elevated cognitive demand. Interpretations of these changes can be provided when considering the role of the SMC and PMC. On the one hand, the SMC's role in voluntary motor tasks is well established (Anwar et al., 2013, 2016a; Guan et al., 2022b; Lutz et al., 2000). In particular, the dlPFC-SMC connectivity has been suggested to be task and muscle specific, only engaging when tasks are considered demanding (Abe & Hanakawa, 2009; Hassan et al., 2014; T. Wu et al., 2008). On the other hand, it is well accepted that the PMC supports both high (cognitive) and low (sensorimotor) level processes (Bonini et al., 2014; Fine & Hayden, 2022; Maranesi et al., 2014; Rizzolatti et al., 2002; Schulz et al., 2019). Keeping in mind that the dlPFC has an important role in executive functioning including planning, working memory, inhibition and attention, the current results could be explained by the following mechanism. As suggested earlier, compared to the altered (virtual) performance, the normal (physical) condition would involve a more complex action-perception cycle (i.e., more complex fine motor manipulations of objects, 3D vs. 2D vision processing, richer sensory feedback). The latter would therefore result in a greater need for

communication between the executive/planning (dlPFC) and the motor (SMC) region to implement the selected action at the sensorimotor level with the help of the premotor (PMC) region which would coordinate the high and low control levels (Abe & Hanakawa, 2009; Alahmadi, 2024; Hassan et al., 2014). When the cognitive demand is small, this discrepancy in cortico-cortical communication between the normal and altered conditions would be limited leading to no observable difference. However, an elevation of the cognitive task demand in the normal condition would not only engage these cognitive functions (e.g., inhibition, working memory, attention) to solve the ToH task but also for sensorimotor (e.g., use attention, working memory during feedback regulation) control. In other words, an elevation of the cognitive task demand would result in a greater need to engage executive functions not only to solve the puzzle but also to implement the sensorimotor functions via the dlPFC-PMC and dlPFC-SMC during the normal condition where the sensorimotor demand is higher relative to the altered condition. In turn, this would result in greater dlPFC-PMC and dlPFC-SMC theta connectivity as the cognitive demand increases in normal condition (Abe & Hanakawa, 2009; Anwar et al., 2013, 2016a; Catalan et al., 1998; Guan et al., 2022b; Hanakawa et al., 2008; Lutz et al., 2000). Conversely, in the altered conditions, simplifying sensorimotor control resulted in diverting less cognitive control resources to sensorimotor processing, and as such enough were available to robustly attend enhanced cognitive demand as indicated by unchanged theta dlPFC-PMC and dlPFC-SMC connectivity under higher cognitive challenge. This result may also suggest that cognitive processing resources engaged to complete the ToH task (e.g., inhibition, working memory, attention) are, to some degree, shared when facing an elevation of

cognitive and sensorimotor demand. This would be consistent with prior studies which revealed that executive functions such as inhibition, working memory, and attention are shared for both cognitive and motor performance (e.g., Feola et al., 2023; Leisman et al., 2016; Marvel et al., 2019). Interestingly, it was previously revealed that inhibitory control resources , which is of primary importance for successful ToH execution (Welsh et al., 1999; Zook et al., 2004), are partially shared through a network involving the prefrontal and precentral regions similar to those examined here (i.e., dlPFC, PMC and part of the SMC) (Feola et al., 2023).The modulations of dlPFC-PMC and dlPFC-SMC connectivity observed here are also consistent with a prior dual-task walking study which revealed a greater fronto-central connectivity in the theta bandwidth between the executive/planning and the premotor/motor regions when individuals executed the task under a higher relative to a low cognitive-motor demand (Shaw et al., 2019). More generally, these results also agree with the notion that an elevation of cerebral cortical networking in the theta bandwidth is indicative of an elevation of the recruitment of processing resources (e.g., working memory, attention, action monitoring) when facing an increase of the cognitive–motor challenge ultimately resulting in an increase of mental workload as it is the case here when comparing the normal and altered conditions (Deeny et al., 2014; Rietschel et al., 2012; Shaw et al., 2019).

Cortico-cortical networking affected by changes in cognitive demand

The elevation of cognitive task demand resulted in an increase of connectivity between dlPFC and both the PMC and SMC. This is consistent with the notion that an elevation of the cognitive demand will result in greater cortico-cortical communication

between the executive/planning (dlPFC) and the premotor/motor (PMC/SMC) regions to select the proper action and then implement it accordingly (Deeny et al., 2014; Rietschel et al., 2012; Shaw et al., 2019). However, the connectivity between the dlPFC-SMC was smaller than the dlPFC-PMC connectivity. While the SMC and its connectivity with dlPFC is rather involved in complex motor execution (Abe & Hanakawa, 2009; Anwar et al., 2013, 2016a; Guan et al., 2022b; Hassan et al., 2014; Lutz et al., 2000; Matsumoto & Tanaka, 2004), the PMC has a more critical function in the interaction between the high- (cognitive) and low- (sensorimotor) level processes (Bonini et al., 2010, 2014; Catalan et al., 1998; Fine & Hayden, 2022b; Hanakawa et al., 2002, 2006; Kansaku et al., 2004; Rizzolatti et al., 2002; Sadato et al., 1996; Schulz et al., 2019). As such, it is possible that the PMC plays a pivotal role in the low-high level interface, at least for this ToH task, leading to a greater exchange of cortico-cortical communication between the dlPFC and the PMC compared to the dlPFC and the SMC; the latter being more motor in nature.

Finally, enhanced PMC-SMC theta connectivity was also observed as the cognitive task demand increased. This enhanced PMC-SMC theta connectivity possibly reflects a greater need to modify the sensorimotor plan (e.g., kinematics, kinetics) as a consequence of more frequent updates of the sub-goals and action selection when trying to execute more complex action sequences (Anwar et al., 2013, 2016; Catalan et al., 1998; Guan et al., 2022; Hanakawa et al., 2002; Lutz et al., 2000; Sadato et al., 1996; Zhang et al., 2010). For instance, if a selected action which consisted of moving a small disk from peg 1 to 2 was updated such that a large disk would be displaced from peg 3 to 1, the sensorimotor plan had to be changed

accordingly. This process is further complicated when more disks and therefore consequences needed to be considered, as in the high demand conditions. Therefore, as the cognitive task demand increases, there is the need for greater coordination between the high- and low-level planning processes. These results are also in accordance with the notion that, as the task becomes more cognitively demanding, an increased theta connectivity would represent enhanced processing resources deployment (e.g., working memory, attention, action monitoring) leading to an elevation of mental workload (Deeny et al., 2014; Rietschel et al., 2012; Shaw et al., 2019). More generally, these findings agree with previous neuroimaging studies which revealed bi-directional effective connectivity (Anwar et al., 2013, 2016a; Bajaj et al., 2014; Rehme et al., 2013) and functional connectivity (Bestmann et al., 2008) between the SMC and PMC which are critical for motor execution of tasks involving the hand.

Conclusions, limitations, and future research

In conclusion, the current effort revealed that both the sensorimotor mapping employed to execute the task as well as the level of cognitive challenge affected the performance and cortical dynamics underlying changes of mental workload. First, the use of a different sensorimotor mapping to complete the task in the normal (physical) and altered (virtual) conditions affected performance as well as both the regional cortical activity and the cerebral cortical networking. Namely, the performance degradation along with an elevation of theta, low-alpha and high-alpha power in the anterior frontal and occipital regions as well as enhanced temporal theta and low-alpha power accompanied with mu rhythm attenuation suggest a greater recruitment of action monitoring, working memory, visual processing, sensory integration, inhibitory and

motor resources in the normal compared to the altered sensorimotor conditions somewhat independently of the cognitive task demand. These regional changes in the engagement of processing resources were also consistent with enhanced dlPFC-PMC and dlPFC-SMC theta connectivity suggesting greater communication between the executive/planning and the premotor/motor regions for the normal relative to the altered condition, respectively. Thus, greater engagement of regional cortical processes and cortical communication resulting in an enhanced mental workload was needed to address the sensorimotor demands for fine motor control and coordination imposed by the richer action-perception cycles inherent to the physical system used during the normal sensorimotor conditions compared to the altered condition where the sensorimotor execution was simplified. It must be noted that the same multi-bandwidth anterior frontal dynamics and central mu-rhythm appeared to be primarily driven by the type of sensorimotor mapping used somewhat independently of the level of cognitive task demands. However, the temporal and occipital theta power were modulated by the execution modality (for both cognitive demand conditions) only when the level of cognitive challenge was experimentally manipulated (i.e., not in the baseline conditions). Importantly, enhanced theta connectivity between the dlPFC and both the PMC and SMC was magnified as a result of increased cognitive task demand only for the normal conditions, not the altered. This suggests that executive processing resources would be, to some extent, shared when facing both cognitive and motor demands.

Furthermore, the level of cognitive task demand modulated behavioral performance as well as both the regional cortical activity and cortico-cortical

communication. Specifically, as cognitive task demand increased the theta power in the anterior frontal, frontal, and occipital regions as well as the FTFA ratio power along with the dlPFC-PMC/SMC and PMC-SMC theta connectivity augmented regardless of the execution modality. The regional cortical theta dynamics suggests greater deployment of attention, action/error monitoring, working memory and visual processes resulting in an elevation of mental workload as cognitive task demand increases. Also, the functional connectivity finding suggests more communication between the executive/planning and the premotor/motor regions as well as between the premotor and motor regions supports the modification of sensorimotor plans driven by sub-goal updates as the level of cognitive challenge increases. Taken together, these results suggest that greater deployment of cognitive-motor resources underlies higher mental workload when normal vs. altered sensorimotor mapping is used or as the cognitive demand increases when executing discrete, sequential tasks. These results may reflect that these resources are mostly separated but the connectivity findings may also suggest that some are shared when facing a combination of both cognitive and motor demand with the PMC playing a central role in successful action sequence performance by supporting the interface between the low- and high-level processes.

Overall, the work presented here contributes to a better understanding of the interaction between the cognitive and motor processes when individuals execute action sequence tasks (similar to many activities of daily living) under various levels of cognitive complexity and sensorimotor mappings. More generally, this work confirms and expands the notion that cognitive and motor control exists on a spectrum rather than separately and is in line with previous work which has implicated the PMC and

SMC in decision-making, error detection, and the integration of sensory information to guide motor actions (Le Bouc et al., 2021) as well as the importance of both areas along with the dlPFC for sequence learning (Nachev et al., 2008) ultimately suggesting a gradual involvement of the dlPFC, PMC, and SMC in response to low- and high-level processes (Abe & Hanakawa, 2009).

Although informative, this work has several limitations. First, while the cortico-cortical networking analysis revealed interesting findings, it was very focused and as such a broader network encompassing the entire scalp should be also considered. Also, the directionality of the regional interactions was not examined and thus could be investigated in the future (e.g., using the directed phase lag index), along with frequency bandwidths beyond theta and alpha. In addition, WPLI has limited capability in regard to capturing local coupling, particularly within sensorimotor circuits such as the link between SMC and PMC as their interactions occur with near-zero phase lag synchrony which is excluded intentionally during WPLI computation. Therefore, future examinations should consider employing methods that can capture interactions that include zero-lag coupling along with the application of source localization methods to minimize the effects of spurious coupling. More generally, future work should examine the relationship between the Levenshtein Distance and EEG dynamics more directly (e.g., linear mixed effect models), as well as the impact of other performance measures (e.g., moves made). Additionally, here EEG modulation was not examined during the motor (i.e., SCTm) and cognitive (i.e., SCTc) time separately nor at different problem-solving states as individuals progressively completed the task. Thus, future work could also conduct more detailed analysis of cortical dynamics during these

different states/stages while also considering possible inter-individuals differences. While this study focused on performance, subsequent work should examine both behavior and cortical dynamics when individuals engage in the practice of action sequence tasks such as the ToH under different conditions. Further, only healthy, young individuals without knowledge of the ToH were considered here and retention and transfer tests were not conducted. The examination of different healthy (e.g., optimal and sub-optimal performers) and clinical populations along with transfer and retention tests would help to better understand the neurocognitive mechanisms underlying the cognitive-motor strategies adopted by individuals when faced with different sensorimotor and cognitive demands. For instance, this work could inform the engagement of cognitive-motor performance in clinical populations such as Veterans who suffer traumatic brain injury. The virtual approach could be deployed in-person or remotely to support continued practice by attenuating the physical limitations and minimizing the necessity for aid, while also promoting involvement in rehabilitation and practice. One limitation of the ToH in a clinical context such as this is that individuals may develop strategies that could aid performance during future assessments. While this is not completely avoidable, learning effects can be minimized by presenting individuals with different initial and end-goal states (Welsh & Huizinga, 2005), adding more pegs or rings, as well as with the introduction of different rules (e.g., disks can only be moved from right to left, clockwise) (Berend & Sapir, 2006), or employing isomorphs of the ToH (Clément et al., 1997). Additionally, the sensorimotor mapping during the altered conditions was based on simple point-and-click controls in a virtual, non-immersive environment (i.e., desktop with computer

mouse). While this allowed for a pointed examination of reduced sensorimotor input compared to normal conditions, it would be interesting to examine how the cognitive-motor processes are modulated when individuals perform sequential tasks using sensorimotor mapping with different controls (e.g., click-and-drag controls, eye-movement, cybergloves), devices that restrict/impair movement, and /or more immersive virtual reality systems (e.g., Oculus™ headset). Last, this work contrasted the physical and virtual execution when individuals executed the task in-person. Therefore, it would be informative, particularly in a tele-medicine context, to examine if the same results would apply if the physical and virtual execution and/or the cortical dynamics are modulated by in-person compared to remote settings. More generally, the results presented here have the potential to inform applications where individuals perform sequential tasks physically and/or virtually. In particular, this work can inform the neurocognitive mechanisms that support performance of sequential tasks of various complexity using physical and virtual systems across many fields such as, but not limited to, human factors, rehabilitation, and telerobotics.

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