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Quantification of Sensory and Cognitive Processes during Multi-Digit Actions in Humans

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Abstract

The continuously varied states of human body and surrounding environment require instantaneous motor adaptations and the understanding of motor goal to achieve desired actions. These sensory and cognitive processes have been investigated as elements in motor control during last five decades. Specially, the task dependency on sensory and cognitive processes suggest the effects of movement properties in terms of environment situation and motor goal. However, these effects were mostly empirically summarized with the measurements of either neural activity or simple motor accomplishment unilaterally. The current thesis addresses the quantification of sensory and cognitive processes based on simultaneous measurements of brain activity and synergic motor performance during multi-digit actions with different movement properties. Multi-digit action as a representation of synergic movements has developed into a widespread agency to quantify the efficacy of motor control, as the reason applied in this thesis.

In this thesis, multi-digit rotation and pressing tasks were performed with different movement directions, frequencies, feedback modalities, or task complexities. (Chapter 3) The changes of movement direction induced a decrease in motor synergy but regardless of which direction. (Chapter 4 and 5) Increased frequency of rhythmic movement reduced synergic motor performance associate with decreased sensory process and less efficient cognitive process. (Chapter 6) More comprehensive feedback modality improved synergic performance with increased sensory process. (Chapter 7) Increased movement complexity had a consistent but stronger effect as increased frequency on synergic performance and efficiency of cognitive process. These observations suggest that several movement properties affect the contributions of sensory and cognitive processes to motor control which can be quantified through either neural activity or synergic motor performance. Accordingly, those movement properties may be applied in the rehabilitation of motor dysfunction by developing new training programs or assistant devices. Additionally, it may be possible to develop a simplified while efficient method to estimate the contribution of sensory or cognitive process to motor control.

Keyword : Sensory process; Cognitive process; Multi−digit actions; Movement properties
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Chapter 1. Introduction

1.1. Problem Statement

The ability of meticulous manipulation in humans is much more excellent than in other animals, which is the foundation of tool utilization and civilization development. However, the manipulation ability can seriously be injured or even broken by neurological impairments such as Parkinson's disease, cerebral paralysis, stroke, or even common aging. Due to the increase of the elderly population and aging-related disorders, the necessity of diagnosis and rehabilitation on the impaired manipulation ability cannot be overestimated. Especially, it is worth promoting if the diagnosis method can be performed in the early stage of ability impairments and in a common situation, for instance, by a test of daily action.

To achieve desired manipulations in daily life, instantaneous motor adaptations and the understanding of motor goal are required due to the continuously varied states of human body and surrounding environment. These sensory and cognitive processes have been investigated as elements in motor control during last three decades (Georgopoulos 2000, Dunn 2001). In addition, the effects of sensory and cognitive processes to motor control and performance are task-depended which suggests the effects of movement properties in terms of environment situation and motor goal. Hence, the quantification of sensory and cognitive processes is an efficient way to investigate the neural mechanism of motor control and the foundation of diagnosis and rehabilitation on those neurological impairments.

Recent studies have verified the existences of sensory and cognitive process in central neural system (CNS) (Leisman, Moustafa et al. 2016, Niutanen, Harra et al. 2020). However, the effects of those two processes were investigated mostly by estimating the accomplishment of mental tasks and simple motor tasks, for instance, finger tapping. These investigations are incapable to interpret the mechanism of motor control in manipulation with multiple degree of freedoms (DOFs). In contrast, those effects in complex movements such as walking were mostly empirically summarized without the measurement of neural activity. Therefore, to estimate the effects of sensory and cognitive processes in complex movements, more evidences in terms of the neural activity are required.

The current thesis addresses the quantification of sensory and cognitive processes based on simultaneous measurements of brain activity and movement performance during multi−digit actions with different movement properties. Multi−digit action as a representation of synergic movements with multiple DOFs has developed into a widespread agency to quantify the efficacy of motor control, as the reason applied in this thesis (Latash and Zatsiorsky 2009). In this thesis, multi−digit rotation and pressing tasks were performed while the brain activity and performance were supposed to be different during tasks with different movement properties as movement directions, frequencies, feedback modalities, or task complexities.

1.2. Study objective

The current thesis attempted to quantify the contributions of sensory and cognitive processes in motor control during multi−digit actions with sundry movement properties. Specifically, following topics were investigated:

(1) Do the contributions of sensory and cognitive processes vary due to the differences in movement property during multi−digit actions? Previous studies have investigated the sensory or cognitive process in mental tasks or simple motor tasks depending on movement properties, for instance, the feedback modality during finger tapping task, the speed of arm reaching, and the magnitude of finger force supposed to be produced (Messier, Adamovich et al. 2003, Stenneken, Prinz et al. 2006, Olivier, Davare et al. 2007). In contrast, motor control of multi−digit actions requires additional

process to deal with the redundant system obtaining multiple DOFs. During last three decades, several approaches were proposed to quantify the control process toward redundant system and verified the task–dependency of that process. Accordingly, sensory and cognitive processes, as the elements of motor control in neural system, were supposed to be varied due to the task–depended motor control during multi–digit actions.

(2) Can the contributions of sensory and cognitive processes be quantified by measurements of neural activity or movement performance? Previous studies have investigated the sensory and cognitive processes in neural activity level through devices utilized in molecular biology, biomedical engineering, and neurological behavior (Gentsch, Weber et al. 2016, Freedman and Ibos 2018, Brooks and Cullen 2019). In contrast, motor control process was investigated in performance level through other approaches in kinesiology, behavior science (Martin, Terekhov et al. 2013). Efforts were continuously made to link the observations in these two levels and improve the understanding of human motor system. Benefit on the development of the mechanical analysis on human movements and the approaches in neurophysiology, it becomes possible to simultaneously measure the neuronal activity of the brain and precise performance during complex movement production. Further, it becomes challengeable to link the neuronal activity and movement characteristics through which to quantify contributions of sensory and cognitive processes to motor control.

1.3. Organization of dissertation

This chapter attempted to introduce the necessity of further understanding of motor control in terms of sensory and cognitive processes. Additionally, neuronal and behavioral measurements during actions with multiple DOFs may be a proper approach to quantify the contributions of these two kinds of processes. Several movement properties were designed to test the task–dependency of those contributions and their effects during multi–digit action in following chapters.

Chapter 2 reviewed the background of this thesis including the introduction of motor system, motor synergy, and motor control. Motor system represents the physiological foundation of the implement of motor control from which the structure and components of motor control process are implied. Motor synergy is a concept focused on the description of approaches and observations in redundant systems with multiple DOFs. Motor control has been investigated through numerous models to understand the relation between task goal, movement implement, neural activity.

Chapter 3 presents the effect of movement direction on motor control during multi-digit force production action (Fig. 1.1) (Park and Xu 2017). Movements are performed by the coordination of two groups of muscles, agonist and antagonist muscles. Different muscle properties such as fiber length and muscle strength in agonist and antagonist muscles challenge the motor control process to coordinate these two groups of muscles during movement in different directions. However, it is questionable whether these peripheral differences are noticed by CNS and cared in sensory or cognitive process.

Chapter 4 and 5 presents the effect of movement frequency on motor control during rhythmic multi-digit rotation and pressing actions (Fig. 1.1). Frequency as a variant of speed has an assignable effect on movement performance distributed in numerous studies about, for instance, speed-accuracy tradeoff as a well-known phenomenon. Both brain activity and movement performance were simultaneous measured to quantify the contributions of sensory and cognitive processes on difference in motor control due to movement frequency. Brain activities were analyzed through the overall magnitude in a wide region in chapter 4 or the time sequence variance in a special region in chapter 5.

Chapter 6 presents the effect of movement modality on motor control during rhythmic multi-digit actions (Fig. 1.1). This chapter focused on the investigation of sensory process through the principle of sensory integration. Accordingly, when the sources of sensory feedback are expanded, the utilization of sensory information is supposed to be raised. However, it is unclear whether that effect on motor control is parallel or resistant with effects of other movement properties, for instance movement frequency maintained in previous chapter. If they are resistant, it is worth investigating the interaction in motor control process.

Chapter 7 presents the effect of movement complexity on motor control during rhythmic multi-digit actions (Figure 1-1). This chapter focused on the investigation of cognitive process by expanding the concept of task difficulty in mental tasks into motor tasks. Difficulty conspicuously increase the load of cognitive process in mental tasks and give negative effect on goal-related behavior. Similarly, the load of cognitive process in motor tasks and its contribution on movement performance are supposed to be changeable.

Finally, chapter 8 provides a summary of above investigations and suggests directions for future researches.

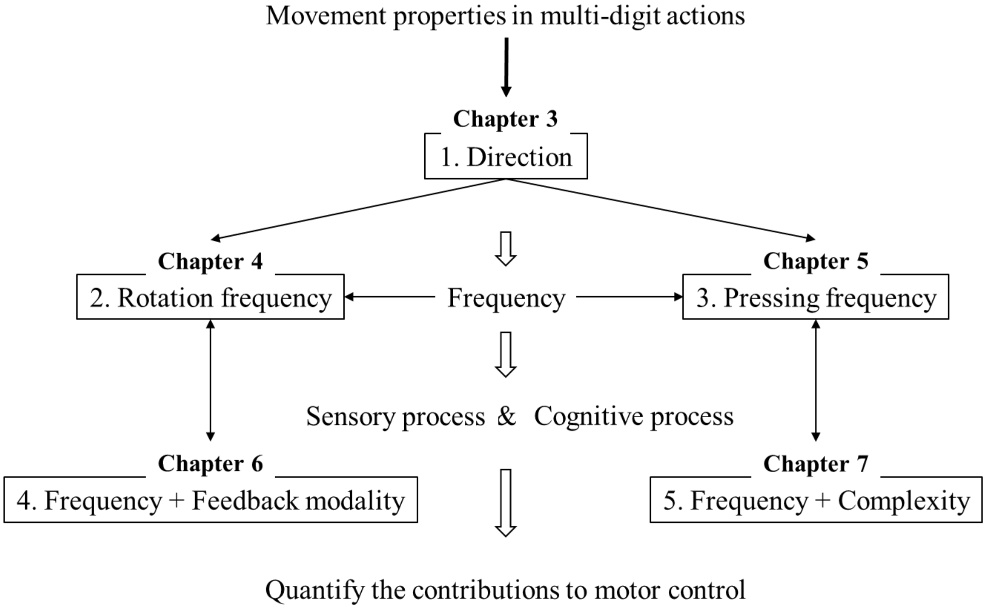

Figure 1-1: Organization of dissertation.

Chapter 2. Background

2.1. Motor System

Human movement is complicated and generated under the coordination of all parts of human body from segments or skeletal muscles in large scale to membrane potential or neurotransmitter in molecule scale (Kandel, Schwartz et al. 2000). The motor system is generally viewed as composed of the CNS, musculoskeletal system, and sensory system where the CNS is hierarchically organized from the cerebral cortex to the spinal cord. Sensory information ascends to the cerebral cortex through the spinal cord while motor signals descends to muscles from the cerebral cortex through the spinal cord. Therefore, the integration of ascending and descending signals exists in the CNS which causes complex neural pathways be called networks. To investigate the connections between movement and neural system, the anatomic pathways within the motor system will be introduced by focusing on the transmission and processing of information during voluntary movement in sights of ascending pathway, descending pathway and brain networks.

2.1.1. Ascending pathway

Initially, information from the external world, the inside of body and the relative configuration of the body segments is the input of motor system (Geldard, O'Hehir et al. 1953). This information is transduced by receptors which are specialized cells or subcellular structures transducing specific types of energy into electrical signals. The receptors can be classified to exterceoptors, interoceptors, and proprioceptors. Modern science recognized five special senses (vision, hearing, balance, taste, and smell) and four general senses (pain, temperature, touch, and pressure) (Woody and Szechtman 2002). The exterceoptors for general sensation are located in the skin including chemoreceptors, mechanicoreceptors, nociceptor, thermoreceptor while the exterceoptors for special sensation are located in the eye, temporal bone, tongue and nose for sensing visual, auditory, vestibular, gustatory, and olfactory information. Besides, there are also similar interoceptors within the respiratory, cardiovascular, endocrine, gastrointestinal, and urogenital systems that sensing internal milieu. Proprioceptors are actively involved in motor function because they are nerves with an axon located at the muscle spindles which scattered among and also composed of muscle fibers. Information about the length of velocity of muscle fibers is elicited by that axon of proprioceptor neurons named sensory endings.

Information transduced by different sensory receptors is transmitted from its peripheral sources to the CNS through different ascending pathways which composed of a series of relay nuclei (Geldard, O'Hehir et al. 1953, Murray and Wallace 2011). The relay nuclei serve to preprocess sensory information and determine whether it is transmitted to the cortex by information intensity. For instance, light arrived at the retina is transduced by photoreceptors and transmitted to the optic nerves located in the retinal ganglion (Rodieck 1979). The optic nerve projects onto the lateral geniculate nucleus of the thalamus which sends information to other brain structures including the cortex. Since eyes are closed to the brain, the vision pathway only contains 3 layers of myelinated nerves and makes the visual information traveling through within 100 milliseconds. Similarly, auditory, vestibular and gustatory information is conveyed to different nucleus of thalamus and finally different regions of brain within a relative short conduction time. Specially, most receptors in the skin and proprioceptors in the muscles correspond with the afferent nerves located at spinal ganglion which carry sensory information to the spinal cord through the dorsal columns and then ascending to ventral posterolateral thalamus (Connor 2004). Comparing to vision pathway or other pathways, this somotosensation pathway contains a number of inter−neurons in the spinal cord and afferent nerves which have a relative long fiber spreading to skin or muscles. Therefore, somotosensation has a longer conduction time within 200 milliseconds to arrive brain depending on which body segment acting in (Prescott and Ratté 2017).

In summary, by traveling through ascending pathways, brain receives multiple sensory information with special latency which is short for information from neighboring receptors like vision and is long for remote receptors like proprioceptors in muscles, especially muscles involved in the movement of limbs.

2.1.2. Descending pathway

After sensory information arrives brain, brain constructs perception and cognition after which the motor signal generated responsible for future movement. Descending pathways act as the function of sending motor signals to muscles to execute movement including both involuntary and voluntary movements. Involuntary movement such as splanchnic activation is out of motor control but under the unconsciously balance by sympathetic and parasympathetic nerves in visceral descending pathway (Sengupta 2009). This section reviews the descending pathways for voluntary movement while the generation of motor command and the process of motor control will be introduced in Chapter 2.3. Voluntary eye movement is quite different from others like prehension or locomotion in both performance and neural networks. There are various mechanisms for moving eyes in several types such as saccadic eye movements, smooth eye movements, vergence eye movements (Radach, Hyona et al. 2003). Signals from a wide region of brain and brainstem are descending to eye muscles without entering spinal cord which causes a short latency and the rapid accurate eye movements.

The major descending pathway consists of two components: upper and lower motor neurons. The pathways from the upper motor neurons in the cerebral cortex, descend and cross over to innervate the lower motor neurons which located in the brain stem or spinal cord (Jacobson, Marcus et al. 2011). The axons of the upper motor neurons either synapse on interneurons or end directly on the lower motor neurons. Corticospinal pathway innervates the motor neurons which send motor signals descending to the skeletal muscles in the neck, thorax, abdomen, pelvis, and the limbs. About 75–90% of the corticospinal tract fibers cross at the medulla−spinal junction and are thereafter found in the spinal cord (Jacobson, Marcus et al. 2011). It appears that many cortical nuclear axons end on interneurons in the spinal cord and not directly on the motor neuron. Finally, motor signals from brain arrive motor neurons whose axon branches in a target muscle and innervates fibers. One motor neuron innervates muscle fibers of several muscles while one muscle consists fibers innervated by several motor neurons. The electrical signals carried by motor neurons, which also be called action potential, lead to the contraction of linked muscles (Latash 2008). Muscle contractions may fuse leading to a smooth tetanus at a high frequency of action potentials which can be measured by electromyography (EMG). Muscle contraction together with passive muscle tension generates muscle force while coordination of various muscles organizes joint moment and drives movement with variable amplitude, direction, and frequency.

2.1.3. Brain networks

Brain networks can be mainly described in two concepts including structural networks, functional connectivity (Fornito, Zalesky et al. 2016). Structural networks address the physical or chemical connections between neural elements such as axons and synapses between neurons in different brain regions. In contrast, functional connectivity describes statistical coordination between neurophysiological signals recorded from different neurons with invasive or non−invasive devices, such as multi−electrode array (MEA), functional magnetic resonance imaging (fMRI), and electroencephalography (EEG). The understanding of structural networks is the foundation in the analysis of functional brain connectivity. This section focus on the introduction of several brain structures involved in motor control. The contribution of functional brain connectivity in large scale involved in motor control of voluntary human movement will be introduced in Chapter 2.3.

Brain is a complex but hierarchical, modular system and can be coarsely divided into cerebrum, diencephalon, cerebellum, brainstem, pons and medulla oblongata. Specially, when focus on cerebrum, the largest part of brain, it can be subdivided into several lobes (i.e. frontal lobe, parietal lobe, temporal lobe, occipital lobe, limbic lobe, and insular lobe) and three lobules (i.e. the paracentral lobule, superior parietal lobule, and inferior parietal lobule) in both two cerebral hemispheres. In a finer scale, cortical areas and subcortical nuclei can be divided into areas according to cytoarchitecture of neuron populations (Brodmann 2007). For instance, primary motor cortex (M1) is defined anatomically as the region of cortex containing special large neurons. These neurons send long axons down to the spinal cord and connect to the interneuron in the spinal cord or directly to the alpha motor neurons who connect to muscles. Prefrontal cortex (PFC) is initially defined as the front part of the frontal lobe based on the presence of a cortical granular layer IV (Uylings, Groenewegen et al. 2003). It also be defined as the region of cortex that has reciprocal projection with the mediodorsal nucleus of the thalamus (Preuss and Goldman‐Rakic 1991). Visual cortex is located in the occipital lobe which receives the sensory input from the lateral geniculate nucleus in the thalamus. According to ventral–dorsal model, visual cortex transmits information through two pathways, one of which goes to inferior temporal cortex while another to the posterior parietal cortex (Ungerleider 1982). The thalamus mentioned above locates in the diencephalon and project nerve fibers to cerebral cortex in lots of directions (Sherman 2006). Additionally, basal ganglia (BG) are a group of subcortical nuclei situated at the base of the forebrain and strongly interconnected with cerebral cortex, thalamus, and brainstem.

These brain structures are interconnected with other brain areas and form the networks in motor system (Redgrave, Rodriguez et al. 2010, Leisman, Moustafa et al. 2016). The large and giant pyramidal cells in the M1 send signals to muscles directly or un-directly and result the contraction of muscles via dorsal BG and brain stem. At the same time, M1 receives information from the PFC, the thalamus, and the sensory cortex including visual cortex. In contrast, the PFC projects in parallel pathways to the M1, ventral BG, and the brainstem while receives projections from the thalamus and the sensory cortex including visual cortex. The essential pathway for BG is that the excitatory from the cerebral cortex transmits to inhibitory of BG and then to excitatory of ventrolateral thalamus and cerebral cortex. The thalamus motioned in both ascending and descending pathways receives information from both sensory cortex and dorsal BG connected with M1.

In summary, some regions of brain receive information from ascending pathway while some other regions send motor signals to descending pathway. Specially, some regions participate in both ascending and descending pathways or connect to other regions inside the brain that conform a complex brain networks. The configuration and function of the brain networks is the key to understand motor control.

2.2. Motor synergy

By reviewing the structure of motor system, it reveals that a great number of cells including nerves, muscle fibers are involved in the motor control. Changes of any one of these cells may lead to different muscle contractions, and therefore muscle force, joint angle or multi-joint limb movements. Logically, it is impossible to control all these neural, muscular, kinetic and kinematic elements one-by-one for every voluntary movement even at every moment. Besides, there are an infinite number of solutions by adjusting these elements to perform a required human task. Nikolai Bernstein realized this redundant degree-of-freedom (DOF) and viewed this redundancy problem as the central problem of motor control (Bernstein 1967). Redundancy problem was formulated as how the

CNS select specific patterns of elements from the infinite solutions equally able to solve the problem. It implies some elements vary together without voluntary effort which has been defined as synergy. The concept of motor synergy was utilized in describing patterns of element variables mainly in three levels: performance, muscles, nerves.

2.2.1. Synergy in performance

Recently, the large number of elements has been considered not as problem but source that allows combination among special properties of performance (i.e. performance variables) for performing actions in the changing environment (Latash 2000). It implies a task-specific stability under which performance variables try to maintain the original trajectory in response to small changes in human body state or external environment. The idea of task-specific stability of actions was originally introduced and developed by Schoner (Martin, Scholz et al. 2009, Scholz and Schöner 2014). If a n-dimensional elemental variable contributes to an m-dimensional performance variable (n > m), there is a (n-m)-dimensional space within which the performance variable does not change its magnitude. This space has been addressed as the uncontrolled manifold (UCM) space. Therefore, the co-variation of elements within the UCM reveals the flexible pattern which has no effect on performance error. In contrast, coordination of elements to reduce the deviations orthogonal to the UCM space (ORT) can reduce performance error which also be called error compensation. The framework of the UCM approach offers a method of quantifying synergies by comparing the amounts of variance within the UCM and orthogonal to it using linear algebra as a computation tool. The UCM is approximated as a linear space and defined as the null-space of the Jacobian matrix which shows how small changes in the element variables affect the performance variable (Scholz and Schöner 2014). This approach has been applied to quantify the synergic actions of element variables in various human actions, for example, multi−joint coordination, finger movements, and postural control (Black, Smith et al. 2007, Latash and Zatsiorsky 2009, Scholz and Schöner 2014). In constant, the task of multi−digit hand movement requires the net kinetics of all fingers but flexible patterns of individual finger kinetics were observed in different tasks. One common phenomenon is finger enslaving as when one of the fingers moves or exerts force other fingers also move or generate force even when they are not required to do that by instruction (Zatsiorsky, Li et al. 2000, Li, Latash et al. 2003, Martin, Latash et al. 2009). The mechanisms of finger enslaving were investigated at least in three sights: (1) structural connections between muscles and tendons in peripheral level; (2) motor units in the extrinsic flexor and extensor muscles connecting multiple digits in joint level; and (3) diverging central commands. The next parts of this chapter will introduce the effect of muscles and CNS commands on synergy.

2.2.2. Synergy in muscles

The notion of muscle synergies was proposed since early twentieth century to describe the stereotypical patterns of muscle activation based on the idea that the brain controls muscles not one by one but in groups (Bizzi, d’Avella et al. 2002). Such groups were supposed to be organized in a flexible, task−specific way, which were relatively similar across healthy population but different in cases of motor dysfunction. Bernstein revisited the idea of synergies and defined them as groups of muscles working together in a coordinated, task−specific manner (Bernstein 1967). Mathematical methods have been developed to identify muscle groups based on linear decomposition techniques such as independent component analysis (ICA), principal component analysis (PCA), and non−negative matrix factorization (NMF) (Naik and Nguyen 2014, Chen, Yuan et al. 2018). Most of these methods recorded activation of muscles using surface EMGs. As mentioned before, EMG measures the action potential generated at motor neurons as the input of muscle activation. Neurons have threshold properties which means the stimulus giving to a neuron does not generate any action potential unless the accumulated magnitude of stimulus is over a threshold value to trigger the depolarization of the neuronal membrane. Based on the observation of the relation between muscle length and force, the thresholds for active muscle force production is considered as varied. The equilibrium point (EP) hypothesis was formed by assuming the thresholds as element variables while muscle contractions change the system towards an equilibrium state (Feldman 1986, Feldman and Levin 2009). Therefore, by prior changing the thresholds of muscles before the movement initiation, the system would naturally accomplish the expected movement until the states of muscles matched the EPs. EP hypothesis has been applied to interpret a number of experiment results and developed into referent configuration (RC) theory to interpret muscle synergies during multi-joint movements (Lestienne, Thullier et al. 2000, St-Onge and Feldman 2004). It suggested that motor control is associated with the setting of neuro properties, as thresholds, and translate it into reciprocal coordination (R command) and co-activation (C command) of muscles, as components of CNS commands. The R command is decided depending on the current state and desired state of the system which is consistent with the notion of error compensation in performance. In contrast, the C command increase the joint stiffness and the ability to resist perturbation which is consistent with the notion of stability in performance.

2.2.3. Synergy in neurons

Opposite to voluntary movements, highly stereotypical, short-latency actions linked to a specific sensory stimulus may be called reflexes (Bizzi, d’Avella et al. 2002, Uylings, Groenewegen et al. 2003). While spinal reflexes acting in hand or limb movements don’t involve brain structures, many other reflexes such as the pupillary reflex, and the vestibular-ocular reflex seen in muscles are controlled from the cranial nerve centers (Leigh and Zee 2015). Considering spinal reflexes, spontaneous coordinated movements can be seen in sleeping or decerebrated spinal animals (Matthews 1959, Petersson, Waldenström et al. 2003). Based on the number of synaptic connections among neurons in the reflex loop, it can be classified as monosynaptic, oligosynaptic, and polysynaptic reflexes. It is more clear for movements with a cyclic pattern of kinetic and/or kinematic variables even without similarly structured input signals from animal brain. By reasonable conjecture, these rhythmic movements may be generated within the spinal cord, and possibly by the interactions between spinal cord neurons and peripheral feedback signals. Experimental studies suggested the existence of autonomous neural structures which can active with a special pattern, for instance, during locomotion and breathing. These structures have been described as central pattern generators (CPGs) (Dietz 2003). However, injury in motor cortex has enormous effects on the performance when locomotor, even make it impossible for both humans and other primates. Recent studies have emphasized the clinical influence of the signals from BG, cerebellum and other brain regions to the neural activation in CPGs (Hemami and Moussavi 2014). In particular, afferent inputs into a CPG may change the pattern of its activity and lead movement changes. Hence, best to knowledge until now, it may be opportune to consider the CPGs as spinal networks coordinating muscles and joints under the motor command descending from brain to perform rhythmic movements. However, the coordination of neurons in cerebellum and their functions in motor control are still under investigation.

2.3. Motor control

Along the investigation of physical motor system and synergic motor performance, the understanding of motor control mechanism has developed from the sight of a single field into multi−discipline. In general, due to the variable states of human body and surrounding environment, motor adaptations based on the sensory information and the understanding of motor goal are required to achieve desired actions. It implied the important roles of the process of sensory information and goal-directed cognition in motor control. Both sensory and cognitive processes, as well as the relation between these two processes, have been investigated in manners of kinesiology, behavior science, system neuroscience, computational neuroscience. Note that sensory and cognitive processes are not independent but performed both in parallel and interactive as introduced below.

2.3.1. Sensory process

Sensory information is the linkage between human body and the environment which provides inputs into motor system at every moment from birth to dead. It is as expected that sensory process involves in multiple stages of motor control including motor planning, motor initiation, motor adaptation, and motor learning. In particular, sensory process during motor planning is associated with the cognition of motor goal, which will be introduced in next chapter.

A typical paradigm of sensory process during motor initiation is stimulus-response during motor selection. Researchers have observed the motor selection in both animals and humans and suggested a dual control system containing goal-directed and habitual/automatic control. When behavior is goal-directed, the behavior is determined primarily by the prediction of possible outcomes of different actions, which is preferred to be considered as cognitive process (Dickinson and Balleine 1994, Balleine and Dickinson 1998). Alternatively, in the case of habitual or automatic control, behaviors were described as motor responses based on the sensory stimulus without consideration of expected outcomes. The outcome of habitual behavior is linked to reflexive stimulus-response associations, which is understood as responding to the sensory stimuli rather than their consequences (Horvitz 2009). Numerous mental tasks recorded the motor selection or the reaction time (RT) under different types of sensory stimulus, such as incompatible stimulus or irrelevant stimulus (Nafcha, Higgins et al. 2016). Incompatible stimulus represents stimulus containing information which is conflict with expected response. For example, during a manikin task, moving the figure toward the location of a positive stimulus or away from the location of a negative stimulus was defined as a compatible behavior (Xia, Wang et al. 2020). In contrary, negative stimulus when moving toward or positive stimulus when moving away from were called incompatible stimulus. Consistent observation in numerous studies showed larger RT elicited by incompatible stimulus than compatible stimulus, which are called stimulus-response compatible (SRC) effect (Lien and Proctor 2002, Krieglmeyer and Deutsch 2010, Xia, Wang et al. 2020). Similarly, irrelevant stimulus also increased RT which is called Simon effect (Lu and Proctor 1995, De Houwer, Crombez et al. 2001). Through measurement of neural activity, these effects of sensory stimulus were confirmed in the early stage of motor control under the involvement of multiple brain regions such as M1, primary somatosensory cortex (S1), dorsolateral BG, amygdala and so on (Lien and Proctor 2002, Redgrave, Rodriguez et al. 2010, Aupperle, Melrose et al. 2015, Neely, Koralek et al. 2018).

Sensory process is also performed in motor adaptation during ongoing actions. Through EMG measurement, a second stage of response was confirmed following the spinal-generated response elicited by perturbation (Kurtzer 2015). This response has defined as long-latency stretch reflexes which occurs with the involvement of S1, M1, other cortical and subcortical brain regions (Matthews 1991, Murray and Wallace 2011, Kurtzer 2015). Specially, it was considered as a type of reflex since it occurs very quickly and exhibits wide range of sophistication, in other words, automatic and required minimal attention (Pruszynski, Kurtzer et al. 2011). Self-paced walking and finger tapping were utilized as paradigms to investigate this rapid and habitual sensory process in motor control. For instance, altered sensory information, such as shifted visual and unexpected auditory stimulus, can elicit motor adaptation with a longer RT than general perturbation during dynamic actions (Matthews 1991, Scott 2004, Diedrichsen, Shadmehr et al. 2010). These observations suggest a continual process of sensory information during ongoing actions which will act immediately in response to sensory alteration. For extremely fast actions, even automatic sensory process can be too slow to adapt actions. Hence, anticipate sensory process is depended to generate excepted actions. Obviously, in this case, the capacity of motor adaptation during ongoing actions is reduced. For instance, skilled typists can type a key stroke averaged less than 100ms which is comparable with the latency of reflex. However, the faster they type the more mistakes they make (Tittelbach, Fields et al. 2008). Another issue in sensory process is the integration of multiple sensory modality since different sensation possess different neural pathway and latency. It is confirmed that the process of vision is relatively slow and accurate comparing with proprioception (Cluff, Crevecoeur et al. 2015). However, the multisensory integration during ongoing actions is still questionable and challengeable. Following the reflexes, voluntary action occurs with the involvement of not only sensory information but also intention. The intentional action predicts the consequence of sensory information associated with activity of prefrontal cortex (Miller and Cohen 2001). Theories have been established to understand the control of voluntary actions associated with cognitive process (Gentsch, Weber et al. 2016) and will be introduced in next chapter.

Experience of reciprocated sensory input and action output can induce successful motor learning acting as more accurate and fast actions. As mentioned above, sensory process involves in rapid and automatic motor selection and motor adaptation. Studies have verified the positive effect of practice on consistent stimulus based response (Pfeuffer, Moutsopoulou et al. 2018) and suggest relatively higher contribution of automatic sensory process after practice (Haith and Krakauer 2018). More complex stimulus-response mapping has been proposed to describe motor selection automatically drove by sensory stimulus after learning (Liefooghe and Verbruggen 2019). Compare to the consequent of learning, the achievement of motor learning is more questionable and incite the interests of scientists. Recently, motor learning is considered as associating with perceptual change and plasticity in sensory system (Ostry and Gribble 2016). Neuroimaging studies provide evidences that sensory networks in the brain change in conjunction with motor skill acquisition during training in motor adaptation tasks such as force−field learning (Vahdat, Darainy et al. 2011, Darainy, Vahdat et al. 2013).

2.3.2. Sensory process

The relation between motor control and cognition has been discussed in last several decades. In modern sight, cognitive process during human actions includes the abstraction of action−related content, the identification of sensory−motor states, and the planning and correction of movements (Gentsch, Weber et al. 2016). Actions with minimum volition were introduced in last chapter. However, cognitive process plays an important role in motor planning, voluntary motor adaptation and motor learning during general human actions.

Instead of automatic motor selection based on sensory stimulus, most daily actions are executed to achieve a motor goal and require deliberate planning before the execution. Obviously, motor planning requires understanding of the goal, which is a cognitive process, and prediction of the relation between motor goal and body state under planned movement. A classic paradigm to investigate this goal−directed motor planning is end−state comfort effect during grasp orientation tasks. For instance, the selection of movement sequence depends on the anticipatory understanding of the object such as the shape, weight, relative distance and so on (Rosenbaum, van Heugten et al. 1996, Herbort and Butz 2012). Similarly, the instruction of target position in reaching or aiming tasks strongly affect the plan of movement trajectory with the involvement of M1, parietal cortex and premotor cortex (Crammond and Kalaska 1996, Hoshi and Tanji 2000, Cui and Andersen 2007). Especially, the performance is more consistent with prediction when there is sufficient time to plan (Daw, Niv et al. 2005). Otherwise, when the decision should be taken very fast, the automatic sensory control contribution much more (Blundell, Uria et al. 2016). In addition, the capacity of skilled and accurate motor planning through cognitive process is not inherent (Claxton, Keen et al. 2003) but learned through experiments since or even before the birth which will be mentioned when introducing the cognitive process in motor learning.

Cognitive process is continuously performed in voluntary motor adaptation during ongoing actions to correct motor outcomes. Internal model theories were proposed to explain the cognitive process based on the internal emulation of motor and sensory processes. In these models, cognitive process is postulated as neural process estimating and anticipating the outcome of efferent copies from prepared motor command (Kawato 1999). To follow, an inverse model will be applied to correct motor command toward an optimal state based on the result of estimation. Internal model and its variants successfully interpreted observations of motor adaptation in multiple situations during fast reaching tasks (Sabes 2000, Takahashi, Nemet et al. 2006, Elliott, Lyons et al. 2017). However, the existence and neural mechanism of internal model and inverse model are still under investigating. Recently, the investigation of interface between cognitive process and motor outcomes has become the interest of scientists from multiple research fields. Prefrontal cortex (PFC) has confirmed as an important role in the formation of cognitive process during motor adaptation. Physically, PFC connects with widely brain regions such as sensory system, motor system, limbic system, and thalamic nuclei. Based on that, PFC receives perceptual sensory information and processes it with the help of the memory formed by previous experiences (Miller and Cohen 2001, Nieder and Merten 2007, Fuster 2015, Markowitz, Curtis et al. 2015). Additionally, anterior cingulate gyrus (ACC) has extensive connections with the motor cortex and lateral PFC and showed activations during cognitive tasks (Barbas and Pandya 1989, Dum and Strick 1991, MacDonald, Cohen et al. 2000). However, the function of PFC-ACC interaction in cognitive process is open for debate. Furthermore, even though there are evident shown the activation of brain regions such as PFC, ACC, BG, and so on, the function of these regions in cognitive process is still under investigation.

A paradigm investigating the cognitive process in motor learning is motor imagery and motor observation. Motor imagery entails the process of imagining the movement in a given task without physically execution, which is cognitive process. Large quantity of studies confirmed that motor imagery can accelerate learning and improve motor performance although the efficiency is less than real practice (Feltz, Landers et al. 1988). Similarly, observing the motor learning procedure of others can activate the same neural circuitry, for example, mirror neurons in PFC (Gallese, Fadiga et al. 1996) responsible for motor planning and execution and a better performance later tested in same task (Mattar and Gribble 2005). As a result, motor learning through cognitive process, as a process of neural activation, is effected by several neural disorders such as developmental coordination disorder (DCD), Parkinson disease (PD) and utilized in the rehibitation. By comparison, selection for end-state comfort (Wilmut and Byrne 2014) and coincident timing judgements using motor imagery (Caçola, Ibana et al. 2016) were worse in subjects with DCD. In contrast, PD patients are gradually forced to rely on their slower and computationally more intensive goal-directed cognitive control, even for the execution of over-trained habitual motor functions (Redgrave, Rodriguez et al. 2010).

In summary, motor control contains sensory and cognitive processes whose contributions are situation-differed and task-depended. The factors of the contributions include the parameters of human body such as fatigue, aging, neural disorders, as well as the parameters of movement such as speed, sensory stimulus, instructions, moving distance. Specially, the effect of these factors on sensory process or cognitive process are different in terms of both neural mechanism and its behavioral consequence. In this thesis, several experiments were designed to investigate motor control procedure in terms of sensory and cognitive processes during movements with different parameters as introduced in following chapters.

Chapter 3. Effect of movement direction: Multi-Finger Interaction and Synergies in Finger Flexion and Extension Force Production

3.1. Abstract

The aim of this study was to discover finger interaction indices during single−finger ramp tasks and multi−finger coordination during a steady state force production in two directions, flexion, and extension. Furthermore, the indices of anticipatory adjustment of elemental variables (i.e., finger forces) prior to a quick pulse force production were quantified. It is currently unknown whether the organization and anticipatory modulation of stability properties are affected by force directions and strengths of in multi−finger actions. We expected to observe a smaller finger independency and larger indices of multi−finger coordination during extension than during flexion due to both neural and peripheral differences between the finger flexion and extension actions. We also examined the indices of the anticipatory adjustment between different force direction conditions. The anticipatory adjustment could be a neural process, which may be affected by the properties of the muscles and by the direction of the motions. The maximal voluntary contraction (MVC) force was larger for flexion than for extension, which confirmed the fact that the strength of finger flexor muscles (e.g., flexor digitorum profundus) was larger than that of finger extensor (e.g., extensor digitorum). The analysis within the uncontrolled manifold (UCM) hypothesis was used to quantify the motor synergy of elemental variables by decomposing two sources of variances across repetitive trials, which identifies the variances in the uncontrolled manifold (V_{UCM}) and that are orthogonal to the UCM (V_{ORT}). The presence of motor synergy and its strength were quantified by the relative amount of V_{UCM} and V_{ORT}. The strength of motor synergies at the steady state was larger in the extension condition, which suggests that the stability property (i.e., multi−finger synergies)

may be a direction specific quantity. However, the results for the existence of anticipatory adjustment; however, no difference between the directional conditions suggests that feedforward synergy adjustment (changes in the stability property) may be at least independent of the magnitude of the task−specific apparent performance variables and its direction (e.g., flexion and extension forces).

3.2. Introduction

The design of the human hand enables us to execute a variety of dexterous hand actions through purposeful adjustment of finger motions or forces in various directions. A single muscle can generate and change its effect by pulling or relaxing along a straight line; however, complex and dexterous movements are generated by net actions of multi−muscles involved in a particular task (Bernstein 1967, Turvey 1990). Thus, hand dexterity is the ability to govern the net actions of multi−muscles involved in task, and the net actions of two groups of muscles create the overall finger flexion and extension by multi−fingers. It has been known that finger flexor muscles (e.g., extrinsic muscles including flexor digitorum profundus, superficialis, and intrinsic palmar muscles), which extend to the phalanges of fingers, develop relatively larger tension as compared to finger extensor (e.g., extensor digitorum, pollicis brevis, pollicis longus, etc) due to a larger cross−sectional area (CSA) in the flexors (Davies, Parker et al. 1988, Jacobson, Raab et al. 1992). Especially, the age−related effect on strength difference between finger flexion and extension was reported (Shim, Oliveira et al. 2007, Hsu 2009, Kapur, Zatsiorsky et al. 2010). The functions of the wrist flexor and extensor, which share their functions with the motions of the fingers, are partially specialized based on the fact that the physiological parameters (e.g., cross−sectional area, fiber length, etc.) of the muscles vary across flexors and extensors (Liu, Liu et al. 2014, Bertelli 2015, van Beek, Stegeman et al. 2018). For human hands, individual fingers can be considered as separate but interdependent force actuators (Fahrer 1981, Kim, Shim et al. 2006, Lieu 2008) for finger flexion and extension. “Interdependent force actuator” in fingers means that individual finger force generations are enslaved to some extent resulting in unintended force production (Zatsiorsky, Li et al. 2000, Danion, Schöner et al. 2003, Li, Dun et al. 2004, Martin, Latash et al. 2009). Because the interdependency and strength of individual fingers are varied between finger flexion and extension, the coordination patterns of individual finger forces may depend on the direction of finger force production.

In many of the daily hand and finger activities, we utilize two or more fingers together to achieve desired actions including net flexion or extension force generation. The use of multi-fingers implies that the individual fingers involved in tasks work together for the successful completion of the tasks. Therefore, the human hand with fingers is an excellent example of kinetic redundancy (Li, Latash et al. 1998, Oliveira, Shim et al. 2006, Kim, Shim et al. 2008). The redundancy implies that the number of elements (fingers) is larger than the number of constraints; therefore, there are redundant degrees of freedoms (DOFs) in the description of the movement system (Bernstein 1967, Latash 2000). In multi-finger tasks, the number of constraints (i.e., the number of required conditions) given by experimental instruction (i.e., motor task) is typically smaller than the number of digits which were actively involved in the tasks (Li, Latash et al. 1998, Zatsiorsky and Latash 2008). Theoretically, therefore, an infinite number of force combinations of multi-fingers can equally be solutions for a specific performance such as total force or moment production. Recently, a computational approach to the coordinated behaviors of multi-elements has been proposed (Scholz and Schöner 1999, de Freitas and Scholz 2010, Scholz and Schöner 2014). The main idea of this approach is that the controller may actively use a redundant set of elements resulting in solution families, and the idea is associated with the principle of motor abundance (Latash 2000, Gera, Freitas et al. 2010, Latash 2012). It has been proposed that the organization of solution families for stable performance is a strategy used by a neural structure, which has been termed as “synergies” (Shim, Latash et al. 2003, Kang, Shinohara et al. 2004, Zhang, Scholz et al. 2008). In general, the existence of synergic actions has been characterized and quantified by the task-specific co-variation across repetitive trials between redundant elements (Latash, Scholz et al. 2002, Scholz, Kang et al. 2003, Friedman, Skm et al. 2009, Delis, Berret et al. 2013). Because finger flexor and extensor have different physiological properties, it is questionable whether the controller strategy that govern the multi-finger system in humans is contingent upon finger force directions.

Another aspect of synergic actions in the redundant human system is feedforward modulation as a stability property. Stability in the human movement system refers to an ability to stabilize important performance variables in task-specific ways by organizing multi-elements in the system. Thus, “good” stability of the human movement system implies “good” ability for stabilizing the system against perturbations, which well fits with the classical definition of stability (Taga 1995, Patla 2004). In a redundant movement system, the stability of performance could be adjusted in both negative (i.e., destabilization) and positive ways without net mechanical outcomes. Indeed, a human being has an ability to adjust a certain neural-related variable(s) or to make a subtle change in a performance variable prior to a virtually detectable action if one knows in advance the information of “when” and “what” for the upcoming tasks (Aruin and Latash 1995, Shiratori and Latash 2001, Mohapatra and Aruin 2013). Thus, the feedforward adjustment is possibly implemented with proper information related to the timing and direction of the planned movements. The virtually detectable action is a consequence of mechanical effects (Kim, Shim et al. 2006, Monjo and Forestier 2014) such as changes in force, torque, muscle activation (Li, Zatsiorsky et al. 2002, Shim, Park et al. 2006, Latash 2010, Sarabon, Markovic et al. 2013). Notably, if a performer is not aware of the timing of a future action, the feedforward adjustment is not observed in a variety of human movements (Zhou, Wu et al. 2013, Togo and Imamizu 2016), and this phenomenon has been termed as anticipatory synergy adjustments (ASAs). The phenomenon of feedforward adjustment has been observed if the movement system is redundant, and the initiation of the change in the performance (i.e., mechanical effect) is triggered by a self-selected stimulation. Recent experiments have shown that the purpose of ASAs is to attenuate the strength of synergies prior to voluntary quick actions (i.e., rapid changes in net performance) (Krishnan, Aruin et al. 2011, Kanekar and Aruin 2014, Togo and Imamizu 2016). It is assumed that the attenuation of the synergy is a purposeful destabilization of the performance in order not to compete for its synergy during a quick change in performances. Previous studies elucidated that the variations in the parameters of ASAs were associated with the strength of synergy and force production capabilities across various populations. For a healthy young group, a drop in the synergy index started about −200 ~ −300 ms with respect to the initiation time for the apparent change in the performance (Olafsdottir, Yoshida et al. 2005, Shim, Olafsdottir et al. 2005, Kim, Shim et al. 2006, Klous, Mikulic et al. 2012). The activation time of ASAs is delayed with aging (Kapur, Zatsiorsky et al. 2010, Wang, Watanabe et al. 2016), fatigue (Singh, SKM et al. 2010), and neurological disorders including Parkinson’s diseases (Bleuse, Cassim et al. 2008, Jacobs, Lou et al. 2009, Park, Wu et al. 2012, Jo, Park et al. 2015), and cortical stroke (Sousa, Silva et al. 2015, Jo, Maenza et al. 2016). Seemingly, the delayed ASAs were well associated with the maximal voluntary contraction (MVC) and synergy strengths. However, parallel changes in the initiation time of the ASAs, synergy strength, and MVC were not obvious in stroke survivals (Jo, Maenza et al. 2016) after strength training (Park, Han et al. 2015), and in a comparison between men and women (Shim, Lay et al. 2004). We assumed that the movements of the finger flexion and extension are very different from their physiological and biomechanical perspectives. Therefore, it is worth investigating if the strength of synergy and its modulation are force direction and strength dependent measures by employing finger flexion and extension tasks.

In this study, we investigated both the flexion and extension efforts of finger actions and changed the force magnitude either to the same or opposite directions in a self-paced manner. We analyzed finger interdependency, multi-finger synergy, and modulation of the synergy index during finger flexion and extension. It is currently unknown whether the organization and feedforward modulation of stability properties in multi-finger actions are affected by force directions and strengths. We hypothesized the following: (1) finger independency will be smaller during the finger extension effort rather than during the flexion effort. (2) the strength of the synergies for the steady-state force production will be stronger during the extension effort rather than during the flexion effort, and (3) the time of the ASAs will differ between conditions when the direction of force changes and when it does not change.

3.3. Method

3.3.1. Subjects

Nine right-handed young male subjects (height: 176.89 ± 6.74 m, mass: 77.89 ± 12.59 kg, age: 24.11 ± 3.69 years) were recruited in this study. The handedness of all participated subjects was right, which was determined by the Edinburgh Handedness Inventory (Oldfield 1971). Prior to the experiment, we interviewed individual subjects to check their handedness and previous history of neuropathies or traumas to their upper extremities. None of the participants had a serious impairment history, and the study was performed in accordance with the recommendation of Seoul National University Institutional Review Board (IRB). The consent was informed, and all participants were requested to sign a consent form according to the procedure approved by Seoul National University IRB.

3.3.2. Apparatus

The flexion and extension forces of four fingers along a single axis were measured with four force transducers (Model 208A03, PCB Piezotronics Inc., Depew, NY, USA) with amplifiers. The force transducers were mounted on a customized aluminum panel (size: 140 × 90 × 5 mm) which was fixed to a wooden board (Figure 3-1A). The panel positioned vertically to avoid the gravitational effect during finger force production. There were four straight slits anteroposteriorly on the aluminum panel to attach the force transducers. Adjacent slots were spaced mediolaterally by 3.0 cm along the z-axis. The subjects were supposed to insert their distal phalanges of the fingers into the thimbles (Figure 3-1A) such that it enabled the subjects to make isometric finger flexion or extension efforts selectively. The experimental frame including the panel and the sensors with the thimble was tilted at 25°. Thus, the initial posture of all the finger joints was slightly flexed. The force signals were conditioned, amplified, and an analog-to-digital converter was used to digitize the force signals at 500 Hz sampling rate using a customized LabView program (National Instrument, Austin, TX, USA).

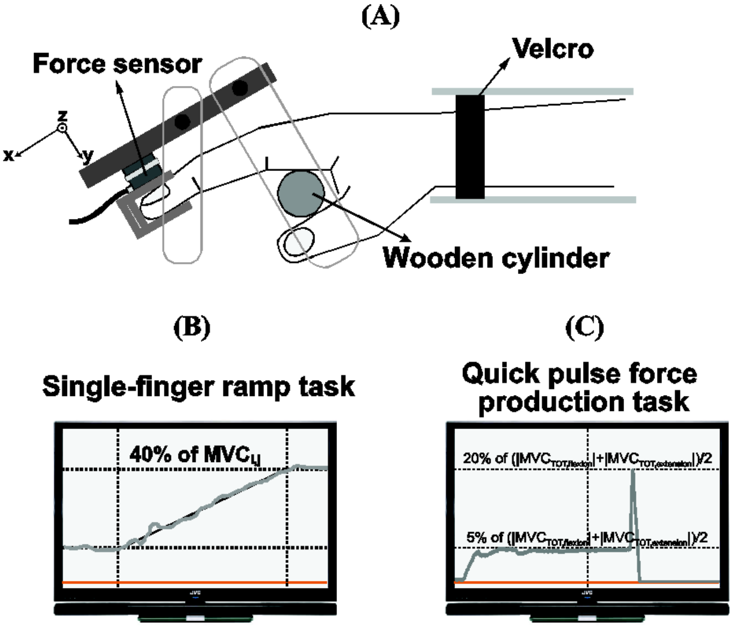

Figure 3-1: Top-down view of the experimental setup in quick pulse force production task.

Top-down view of the experimental setup (A). The subject's wrist was held stationary with Velcro straps. A wooden cylinder supported the palm, and the force sensors were attached to a frame. The feedback screen displayed the real-time finger forces and showed the templates during single-finger ramp tasks (B) and quick pulse force production tasks (C).

3.3.3. Procedures

The subject sat in a height adjustable chair facing computer monitor for a real-time force feedback. The subject abducted the upper arm by about 45 degrees and flexed about 45 degrees with the elbow flexion about 45 degrees. The wrist position was positioned between pronation and supination with respect to the neutral position of the wrist. The total duration of the experiment for each subject was approximately 2 hours. The 1-min break was given between every two trials.

There were three experimental blocks. The first block was the maximal voluntary contraction (MVC) tasks using single-finger and multi-fingers. Subjects were instructed to make isometric flexion or extension efforts as hard as possible with single-finger (I, M, R, L) and all four fingers (TOT), separately. During single-finger MVC tasks, the subjects were not allowed to lift non-task fingers on the corresponding sensors. The force feedback of the task-finger force was visualized on the computer screen (24-inches, 1920 × 1080 resolution at 60 Hz). 8 s were given to the subject to reach their maximum flexion or extension efforts. Each subject performed three trials at the MVC task for each condition. The maximal finger forces ($MVC_{i,j}$; i = {I, M, R, L, TOT}, j = {flexion, extension}) were captured within 8 s, and $MVC_{TOT,j}$ and $MVC_{i,j}$ were used to decide target force levels in the next two tasks.

The second task, the single-finger ramp force production tasks, required the subject to make either extension or flexion effort (j) with one finger (i) and to follow the template shown in the screen. The template on the computer screen consisted of three phases including a 4-s horizontal line at 0% of $MVC_{i,j}$, 12-s slanted line starting from 0% to 40% of $MVC_{i,j}$, and the 4-s horizontal line at 40% of $MVC_{i,j}$ (Figure 3-1B). The instruction to the subjects was that "keep all the fingers on the corresponding sensors and do not pay attention to unintended force production by non-task fingers." We measured both task and non-task finger forces.

The third task was a multi-finger steady state (SS) force production followed by a quick pulse force production tasks. The subjects were given four combinations of "steady state" and "quick pulse" pairs regarding the directions of the finger forces: 1) flexion-flexion (FF), 2) flexion-extension (FE), 3) extension-flexion (EF), and 4) extension-extension (EE). The first letter in the naming of four conditions means the direction of finger force at SS, while the second letter means the direction of finger force for the quick pulse. Note that 2) and 3) conditions required to change the directions of finger force from flexion to extension or vice-versa in which they made a quick pulse force. The subjects were required to press the transducers with all four fingers simultaneously and to maintain a steady-state level for at least 5 s. After the SS force production, the subjects were instructed to produce a quick pulse force to the target within the next 5 s. Note that the initiation of a quick pulse force was not triggered by an external cue but by a self-selected cue. Also, the force direction information for both SS and quick pulse was given to the subject in advance using a template on the computer screen, so the subjects produced the tasks with in advance information of force direction and timing. The magnitudes of the SS force was set at 5% of $(|MVC_{TOT,flexion}|+|MVC_{TOT,extension}|)/2$. The change in force magnitude from "steady state" to "quick pulse" was set at 20% of $(|MVC_{TOT,flexion}|+|MVC_{TOT,extension}|)/2$ for all four conditions. In other words, the task space in the constrained flexion and extension force magnitudes was symmetrical, and magnitude difference between the SS and the quick pulse was the same for all four conditions. The computer screen for the real-time force feedback showed the first force level for the steady-state and the target force level for the quick pulse along the horizontal lines (Figure 3-1C). About 10 – 20 min practice time provided to each subject before data collection. The subject performed 25 for each condition. Thus a total of 100 trials (25 trials × 4 conditions), and the 10-s break between every two trials was provided.

3.3.4. Data Analysis

- Initial data processing

Customized MATLAB (MathWorks Inc., Natick, MA, USA) codes were written to process the measured force data. Before variable computation, the raw signals were digitally low-pass filtered at 10 Hz cut-off with zero-lag, 4th-order Butterworth filter. The following variables were computed to test the formulated hypotheses.

- Enslaving matrix

The enslaving matrix (E) was calculated using the force data from the second task, the single finger force production tasks (Scholz, Danion et al. 2002, Kang, Shinohara et al. 2004). The elements in the E represent the relative amount of forces by non-task fingers, which assumed to be produced unintentionally, to the total force (F_{TOT}) by all four fingers. A linear regression analysis was performed to compute the regression coefficients (e in Eq. 1) between individual finger force (F_i) and F_{TOT} over ramp duration. Then, 4 by 4 enslaving matrix (E in Eq. 2) was composed for flexion(E_{flx}) and extension (E_{ext}) task separately.

$$F_{i,j,k} = f^{0}_{i,k} + e_{i,j,k} \cdot F_{TOT,j,k}, \qquad (1)$$

$$\boldsymbol{E}_k = \begin{bmatrix} e_{I,I,k} & e_{I,M,k} & e_{I,R,k} & e_{I,L,k} \\ e_{M,I,k} & e_{M,M,k} & e_{M,R,k} & e_{M,L,k} \\ e_{R,I,k} & e_{R,M,k} & e_{R,R,k} & e_{R,L,k} \\ e_{L,I,k} & e_{L,M,k} & e_{L,R,k} & e_{L,L,k} \end{bmatrix}, \qquad (2)$$

where i = {I, M, R, L}, j = {I, M, R, L}, and k = {flx, ext}. i and j represent non-task and task finger, respectively. k indicates a force direction. $F_{i,j,k}$ and $F_{TOT,j,k}$ represent the individual i−finger force and total force by all four fingers, respectively, when j−finger was the task finger during k−force direction condition. Also, the averages of the off−diagonal components in both E_{flx} and E_{ext} for j−finger (task finger) were computed ($EN_{i,k}$), which represent the total amount of finger force enslaving (Eq. 3).

$$EN_{j,k} = \sum_i e_{i,j,k}/3 \quad (i \neq j) \tag{3}$$

- Quick pulse force production tasks

Prior to the variable computation, we screened and deleted erratic trials to ensure that those trials did not sway the outcome variables. Especially, the trials, which showed multiple peaks or non−constant (not stabilized) force during steady state period, were excluded from the following analysis. The time of initiation of total force (FTOT) change (t0) was identified in the particular trial, and t0 was used as a reference time moment to calculate the time of the direction of total force (FTOT) changed (tch) and of the peak pulse force (tpeak) (Figure 3.2). t0 was quantified as the time when dFTOT/dt (the first derivative of the total force) reached 5% of its peak value in each trial. Further, average (AvgT) and standard deviation (SdT) of tch and tpeak across repetitive trials in each subject and condition were calculated. For the repetitive trials, the data were aligned with respect to t0, the time initiation of total force change. The co−variation of hypothetical commands to four fingers, i.e., multi−finger synergy, was quantified based on the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999, Latash, Scholz et al. 2002, Scholz, Danion et al. 2002) using the sets of time aligned trials for each subject and condition. Finger modes (m), which are assumed to be the hypothetical commands to fingers, was computed using the E and individual finger forces for each time sample (Fahrer 1981). We assume that the hypothetical commands to four fingers are independent to each other and E matrix represent interdependency among finger force production. Thus, the independent commands (i.e., mode vector) to four finger can be achieved by multiplying two matrices, the inverse of E matrix and individual finger force vector (Eq. 4). A mode vector reflects intended finger involvement of all four fingers by commands. Therefore, the UCM analysis with mode vectors enable us to infer how the neural commands to the fingers are organized to perform the given tasks (Scholz and Schöner 1999, Latash, Scholz et al. 2002). Since we assumed that the interdependency of finger force production was a direction-dependent quantity, we applied Eflx and Eext selectively according to the direction of total finger force.

$$\mathrm{m} = [\boldsymbol{E}]^{-1}F; F = [f_I, f_M, f_R, f_L]^T \tag{4}$$

The variances of time series within two subspaces, V_{UCM} and V_{ORT}, across the repetitive trials for each condition were quantified using force (F) and mode (m) vectors, separately. The mode or force vectors observed in the UCM space confirming to the variance (V_{UCM}) across trials did not affect the magnitude of the performance variable. On the contrary, the orthogonal variance (V_{ORT}) refers to the variability of performance across trials which was produced by the combination of finger forces. Briefly, a synergy index (ΔV) was quantified as the relative amount of V_{UCM} in the total variance, V_{TOT} (Eq. 5). Note that the sum of V_{UCM} and V_{ORT} was equal to the total variance, V_{TOT}. Further, the variances were normalized by the degrees of freedoms (DOFs) of the corresponding spaces (Oldfield 1971, Friedman, Varadhan et al. 2009, Arpinar-Avsar, Park et al. 2013)

$$\Delta V(t) = \frac{V_{UCM}(t)/3 - V_{ORT}(t)/1}{V_{TOT}(t)/4} \tag{5}$$

Before statistical tests, Fisher's z-transformation was applied to ΔVs (ΔV_Z) since ΔVs were constrained by their computational boundaries. The steady state (SS) was set as the period 600-400 ms before t0 (Figure 3-2) (Park, Lewis et al. 2013, Park, Lewis et al. 2014). Two indices were quantified in the period of anticipatory synergy adjustments (ASA): the time of initiation of the ΔV drop (t_{ASA}) and the change in the synergy index ($\Delta\Delta V_{t0}$) between SS and t0. Further, the drop magnitude of the synergy indices ($\Delta\Delta V_{peak}$)

between the SS and negative peak of ΔV after t0 (Figure 3−2) was quantified. The mean and standard deviation (SD) of ΔVZ were computed over the period of SS; t_{ASA} was defined as the time when ΔV_Z dropped below its average SS value by more than 2SDs

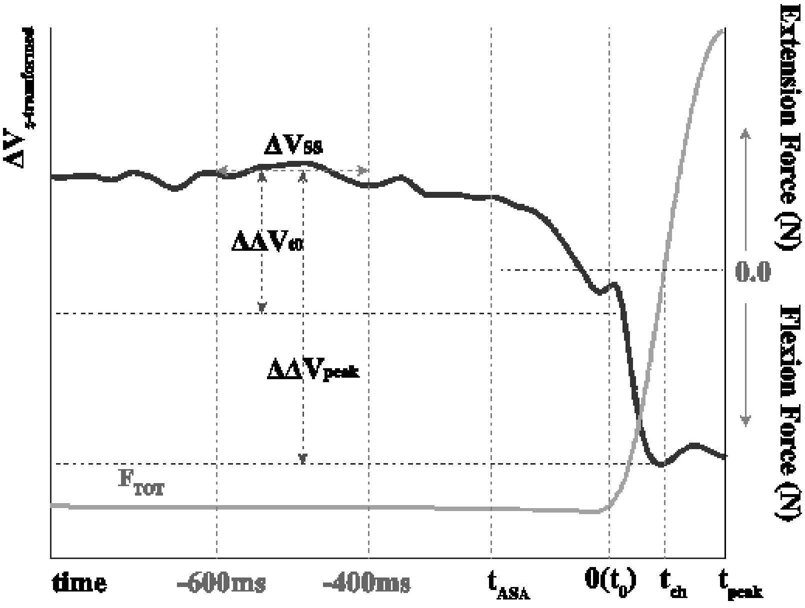

Figure 3−2: The sample data of total force and variance of the total force.

The sample data of total force (gray line) and variance of the total force (z−transformed ΔV, black line) during quick pulse force production tasks. Flexion forces are presented as negative, and extension forces are presented as positive. t_{ASA}, t_0, t_{ch}, and t_{peak} stand for the time of anticipatory synergy adjustment (ASA), the time of initiation of total force(F_{TOT}) change, the time of the direction of force changed, and of the peak pulse force, respectively. ΔV_{SS} represents average ΔV at a steady state. $\Delta\Delta V_{t0}$ and $\Delta\Delta V_{peak}$ stand for the change in the synergy index between steady state and t0 and between the steady state and negative peak of ΔV after t0, respectively.

3.4. Results

3.4.1. Maximal voluntary contraction (MVC) force and finger independency

The maximal voluntary contraction (MVC) finger force during flexion was about two times larger than the MVC force during extension ($F_{[1,\ 8]} = 23.35$, $p < 0.01$). On average ($n = 9$), the MVC_{TOT} forces during flexion and extension were 102 N and 56 N, respectively. Individual finger forces were also larger during flexion than during extension. The order of individual finger MVC forces during flexion ($MVC_{i,\ flexion}$) was I (40 N) > M (30 N), R (26 N) > L (17 N). The order of $MVC_{i,\ extension}$ was I (22 N), M (19 N) > R (15 N), L (9 N). These findings were supported by a two-way repeated measure ANOVA with factors Finger (four levels: Index, Middle, Ring, and Little) and Direction (two levels: flexion and extension), which showed significant main effects of Direction ($F_{[1,\ 8]} = 27.30$, $p < 0.01$) and Finger ($F_{[3,\ 24]} = 22.86$, $p < 0.01$) with a significant interaction of Finger × Direction ($F_{[3,\ 24]} = 3.86$, $p < 0.05$).

Unintended finger force productions by non-task fingers during the single-finger ramp tasks were prominent during both finger flexion and extension. Further, the index of enslaving (EN) was computed, and the EN was larger in the extension condition than in the flexion condition for all four fingers (Figure 3-3). Also, EN of the index finger was smaller than the ENs of other three fingers for both flexion and extension conditions (Figure 3-3). A two-way repeated measure ANOVA with factors Finger (four levels: Index, Middle, Ring, and Little) and Direction (two levels: flexion and extension) showed main effect of Direction ($F_{[1,\ 8]} = 73.44$, $p < 0.001$) and Finger ($F_{[3,\ 24]} = 16.36$, $p < 0.01$) with a significant interaction of Finger × Direction ($F_{[3,\ 24]} = 3.73$, $p < 0.05$). Pairwise comparisons showed that ENI, $EN_M < EN_L < EN_R$ ($p < 0.05$) during finger flexion and $EN_I < EN_M$, EN_R, EN_L ($p < 0.05$) during extension (Figure 3-3), which reflected a significant Finger × Direction.

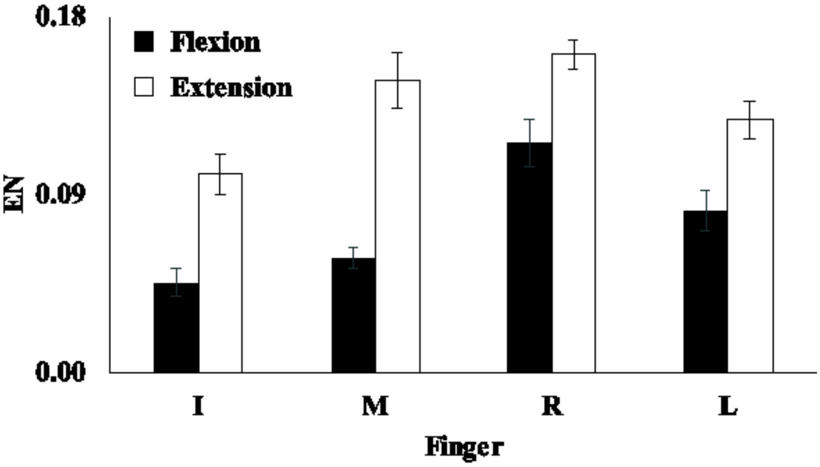

Figure 3-3: The index of enslaving (EN) of four fingers during flexion and extension conditions.

The index of enslaving (EN) of the index (I), middle (M), ring (R) and little (L) fingers during flexion (filled bars) and extension conditions (open bars). Average values are presented with standard error (SE) bars. EN_I, EN_M < EN_L < EN_R during finger flexion ($p < 0.05$) and EN_I < EN_M, EN_R, EN_L during extension ($p < 0.05$).

3.4.2. Timing indices

An average time to reach peak pulse force ($AvgT_{peak}$) across repetitive trials was faster in EF (extension to flexion) than in FF (flexion to flexion) (Figure 3-4A) while there was no difference on $AvgT_{peak}$ between FE (flexion to extension) and EE (extension to extension). $AvgT_{peak}$ for EF and FF were 0.135 and 0.162 s, respectively. The standard deviation of t_{peak} (SdT_{peak}) across repetitive trials was smaller when the conditions required to change the direction of finger force from flexion to extension or vice-versa for a quick pulse force production. In other words, SdT_{peak} of EF (extension to flexion) was smaller than that of FE (flexion to extension), and SdT_{peak} of FE (flexion to extension) < SdT_{peak} of EE (extension to extension) as shown in Figure 3-4B. These findings were supported by a two-way repeated measure ANOVA with factors $Direction_{SS}$ (two levels: flexion and extension) and $Driection_{pulse}$ (two levels: flexion and extension), which showed the main effect of Direction$_{SS}$ ($F_{[1, 8]} = 6.74$, $p < 0.05$) on AvgT$_{peak}$ with a significant Driection$_{SS}$ × Driection$_{pulse}$ ($F_{[1, 8]} = 6.74$, $p < 0.05$). Two main effects on SdT$_{peak}$ were not significant, while the factor interaction Direction$_{SS}$ × Driection$_{pulse}$ on SdT$_{peak}$ was significant ($F_{[1, 8]} = 4.21$, $p < 0.05$). The significant interaction reflected the fact that SdT$_{peak}$ of FF > SdT$_{peak}$ of EF ($p < 0.05$) and SdT$_{peak}$ of FE < SdT$_{peak}$ of EE ($p < 0.05$). In addition, we computed the average (AvgT$_{ch}$) and standard deviation (SdT$_{ch}$) of time of change in the direction of force (t_{ch}) with respect to t0, the time of initiation of F_{TOT} change. AvgT$_{ch}$ was 0.098 for the EF condition (extension to flexion) and 0.109 for the FE condition (flexion to extension), but the difference did not reach statistical significance ($F_{[1, 8]} = 2.83$, $p = 0.13$). There was no significant effect on SdT$_{ch}$.

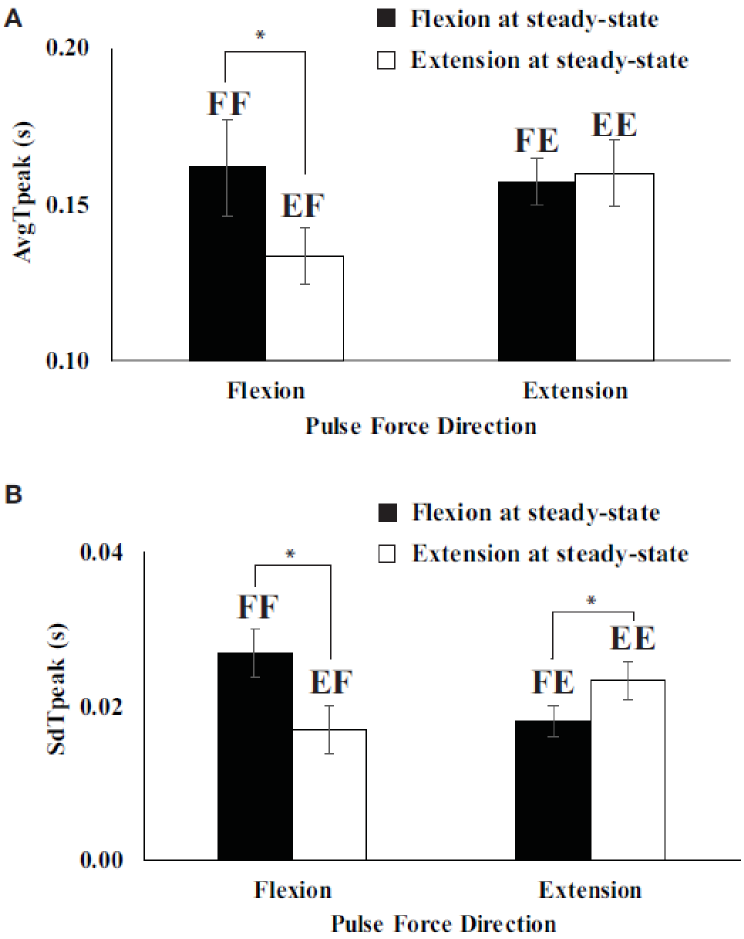

Figure 3-4: Average and standard deviation of the time to reach peak pulse force.

Average ($AvgT_{peak}$) (A) and standard deviation (SdT_{peak}) (B) of the time to reach peak pulse force across repetitive trials when the direction of steady state force was flexion (filled bars) and extension (open bars). Two capital letters above the bars represent the experimental conditions. The first letter represents the force direction at the steady state, and the second letter stands for the direction of quick pulse force. “F” and “E” stand for flexion and extension, respectively (e.g., FF represents “flexion” to “flexion”). Averaged across subjects’ data are shown with standard error bars. The asterisks (*) show statistically significant differences between conditions ($p < 0.05$).

3.4.3. Multi-finger synergy indices in mode space

In the mode space, the indices of the steady state (SS) force stabilization synergies (ΔV_{SS}) were larger during the extension effort than during the flexion effort regardless of the directions of peak pulse force (i.e., EF & EE > FF & FE in Figure 3-5A), which was confirmed by the main effect of $Direction_{SS}$ ($F_{[1, 8]} = 26.77$, $p < 0.01$) without a significant interaction of $Direction_{SS} \times Direction_{pulse}$. In general, the variance in the UCM (V_{UCM}) is larger than the variance in the orthogonal space (V_{ORT}) for all four conditions at the SS ($p < 0.01$), which confirmed the existence of the force stabilizing synergy (Figure 3-6). Thus, ΔVSS difference between the flexion and extension conditions in the mode space was mainly caused by the larger V_{UCM} during the extension effort than the flexion effort, and there was no significant difference in V_{ORT} between the conditions. This result was confirmed by two-way repeated-measure ANOVAs separately on V_{UCM} and V_{ORT} with factors $Direction_{SS}$ (two levels: flexion and extension) and $Direction_{pulse}$ (two levels: flexion and extension). The main effect of $Direction_{SS}$ on V_{UCM} was significant without a factor interaction ($F_{[1, 8]} = 5.68$, $p < 0.05$) (Figure 3-6A), while main effects and factor interaction were not statistically significant on V_{ORT} (Figure 3-6B).

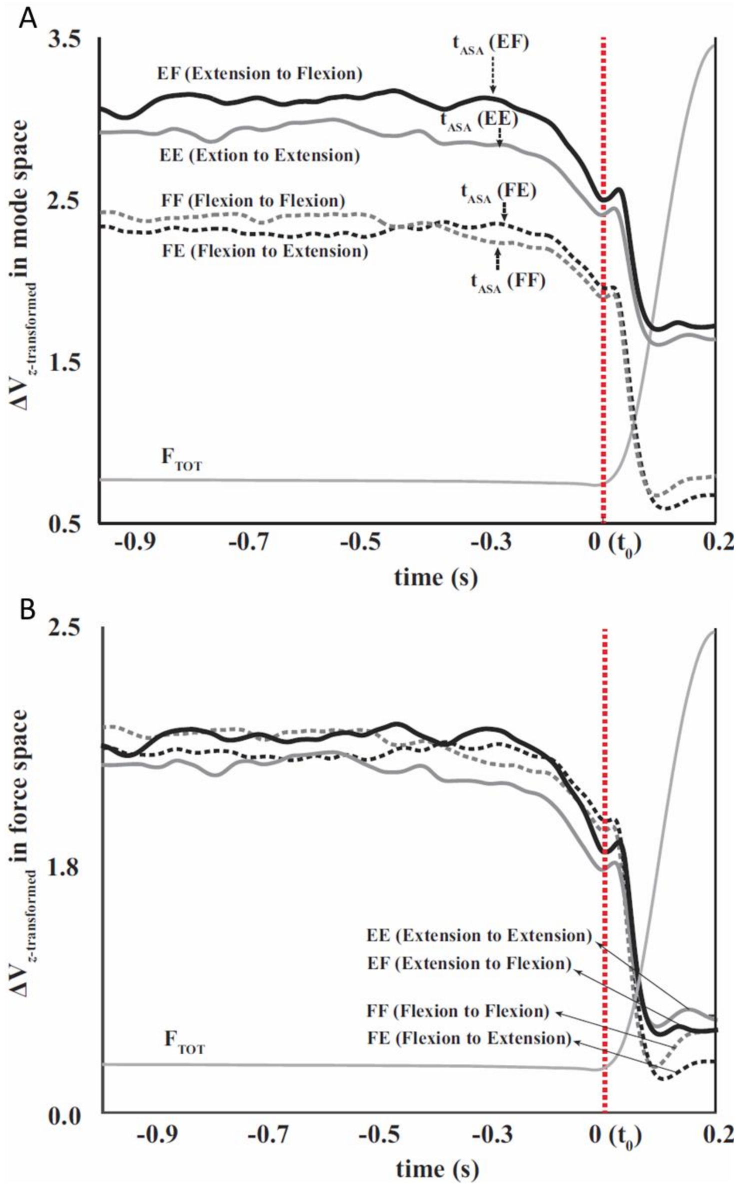

Figure 3-5: The total force and z-transformed synergy index in mode space and force space.

The total force (F_{TOT}, thin gray lines) and z-transformed synergy index (ΔV_Z) during FF (gray dotted line, flexion to flexion), FE (black-dotted line, flexion to extension), EF (black solid line, extension to flexion), and EE (gray solid line, extension to extension) in mode space (A) and force space (B). Averages across subjects are presented for ΔV_Z. The times of ASA initiation

(t_{ASA}) are shown with the arrows.

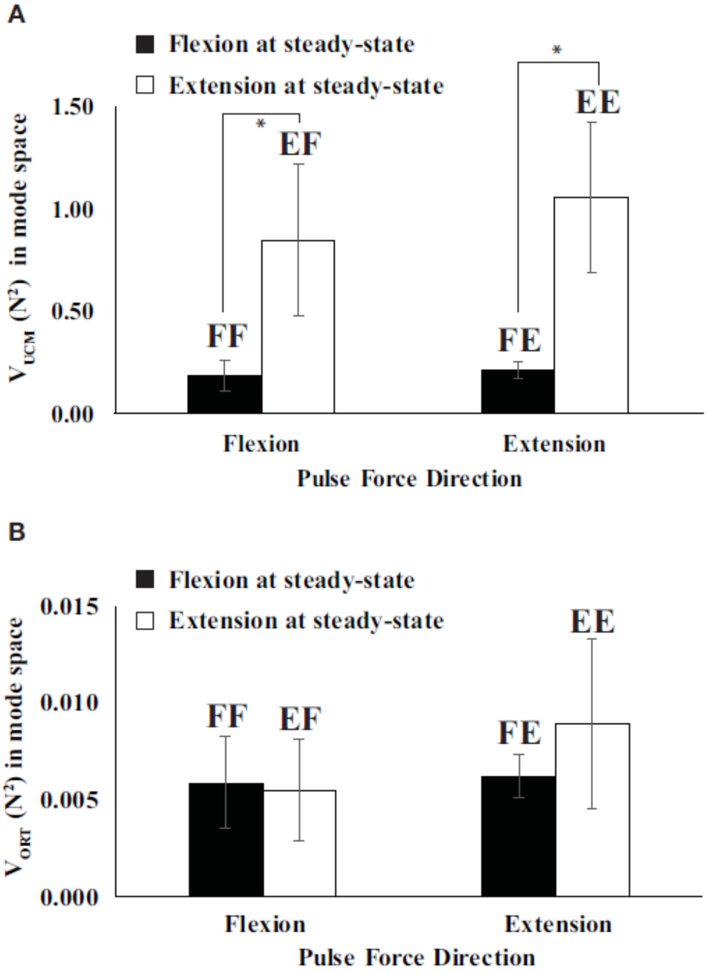

Figure 3-6: The variances in the UCM and orthogonal space.

The variances in the UCM (V_{UCM}) (A) and orthogonal space (V_{ORT}) (B) when the direction of steady state force was flexion (filled bars) and extension (open bars). Two capital letters above the bars represent the experimental conditions. The first letter represents the force direction at the steady state, and the second letter stands for the direction of quick pulse force. "F" and "E" stand for flexion and extension, respectively (e.g., FF represents "flexion" to "flexion"). Averages across subject's data are shown with standard error (SE) bars. The asterisks (*) show statistically significant differences between conditions ($p < 0.05$).

In all four conditions, it was evident that the synergy index started to drop before the initiation of the force pulse and reached its negative peak before the time of F_{peak}. We quantified three indices during and after the anticipatory synergy adjustment, the time of the anticipatory synergy adjustment (t_{ASA}), the difference in the synergy indices between SS and t0 ($\Delta\Delta V_{t0}$), and the difference in the synergy indices between SS and negative peak ($\Delta\Delta V_{peak}$). There was no significant difference on t_{ASA} (Figure 3.5A) and $\Delta\Delta V_{t0}$ between the conditions with no factor interactions. On average, t_{ASA} was about 0.28 s, and the magnitude of the drop in the synergy index during the ASA was not statistically different between the conditions. The $\Delta\Delta V_{peak}$ was larger when the direction of finger force at the SS was a flexion (i.e., a larger drop in the flexion), and this result was not affected by the direction of finger force at the quick pulse. A two-way repeated measure ANOVA with factors Direction_{SS} (two levels: flexion and extension) and Driection_{pulse} (two levels: flexion and extension) supported these finding confirming the main effect of Direction_{SS} ($F_{[1, 8]} = 13.60$, $p < 0.05$) on $\Delta\Delta V_{peak}$ without a significant interaction (Figure 3-7A).

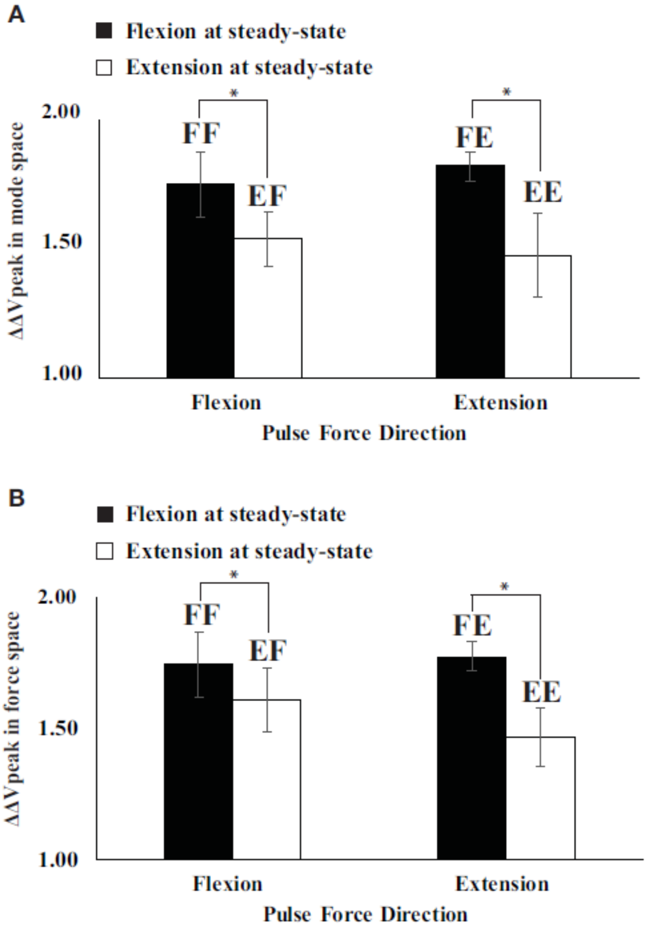

Figure 3-7: The difference in the synergy index between steady state and negative peak.

The difference in the synergy index between steady state and negative peak ($\Delta\Delta V_{peak}$) for four conditions of FF (flexion to flexion), FE (flexion to extension), EF (extension to flexion), and EE (extension to extension) in mode space (A) and force space (B). Averaged data across subjects with standard error (SE) bars are presented. The asterisks (*) show statistically significant differences between conditions ($p < 0.05$).

3.4.4. Multi-finger synergy indices in force space

The same set of variables in the mode space analysis was used for the analysis using the data in the force space. In general, ΔV, V_{UCM}, V_{ORT} at the SS, and $\Delta\Delta V_{t0}$ were not statistically different between the conditions, and factor interactions were also not significant (Figure 3-5B). However, $\Delta\Delta V_{peak}$ was larger when the direction of finger force at the SS was a flexion, which was similar to ΔΔVpeak pattern in the mode space analysis (Figure 3-7B). This finding was supported by a two-way repeated measure ANOVA with factors Direction_{SS} (two levels: flexion and extension) and Driection_{pulse} (two levels: flexion and extension), which showed the main effect of Direction_{SS} ($F_{[1,\ 8]} = 10.17$, $p < 0.05$) on $\Delta\Delta V_{peak}$ without a significant interaction.

3.5. Discussion

The two hypotheses formulated in the Introduction were supported by the results of this study. The third hypothesis about the anticipatory synergy adjustment during flexion and extension was rejected. The actions of fingers were more independent (i.e., smaller enslaving index, EN) during finger flexion than during finger extension, which supports the first hypothesis. The second hypothesis was supported by the results that the strength of synergy index was larger for extension than for flexion in the mode space although the force space analysis showed no statistical difference. The anticipatory synergy adjustment was observed in all four experimental conditions although there was no significant difference between the conditions, which rejects the third hypothesis. The following sections will focus on the possible mechanism of the force direction-dependent changes in the finger independency, stability indices, and anticipatory changes in the stability properties.

3.5.1. Finger independency during finger flexion and extension

Unlike the actions of robotic fingers where individual fingers have separate actuators, the fingers of a human hand cannot make actions independently (Fahrer 1981, Häger-Ross and Schieber 2000, Lang and Schieber 2004) resulting in “voluntary” but “unintended” finger actions. This observation has been termed as enslaving or enslavement (Zatsiorsky, Li et al. 2000, Kim, Shim et al. 2008). The enslaving has been used as an index of finger interdependency and attributed to biomechanical and central factors. The biomechanical factors include an anatomical connection (i.e., passive connection) within the hand and forearm, which induces mechanically coupled actions of fingers (Häger-Ross and Schieber 2000, Schieber and Santello 2004). The central factors for the enslaving include divergence and convergence of cortical projections due to overlapping digit representation in the hand area of the primary motor cortex (Schieber 1990, Schieber and Hibbard 1993). A series of previous studies has reported a significant relationship between the voluntary force production capability (i.e., MVCs) and finger force enslaving. One group of studies reported a positive correlation between enslaving and MVC (Danion, Latash et al. 2000, Danion, Latash et al. 2001, Shinohara, Li et al. 2003), which is likely enslaving increased by the magnitude of the MVC, which was opposite to the results of this study. The subjects in those studies were healthy individuals with different levels of finger strengths (e.g., young, healthy-aged elderly, females, and fatigued subjects). The other group of studies provided evidence of the counterexamples of a positive correlation between MVC and enslaving. A higher enslaving was observed in individuals with neurological disorders such as Parkinson’s disease, cerebellar disorder, and stroke (Cho, Min et al. 2010, Park, Lewis et al. 2013, Jo, Park et al. 2015) whose MVC forces were smaller than age- and gender-matched controls. The higher enslaving with lower MVC forces in groups with neurological diseases is probably led by central factors rather than peripheral (biomechanical) factors (Park, Lewis et al. 2013, Park, Lewis et al. 2014). However, it is still questionable as to the relative contributions of peripheral and central factors to enslaving (and MVC forces) in healthy peoples. In our study with healthy individuals, the higher enslaving was accompanied by a lower MVC force during finger extension, which was a similar enslaving pattern to that found in patients with neurological disorders. By combining the abovementioned studies, the higher enslaving during finger extension may be a consequence of both peripheral and central reasons; however, the contribution of the supraspinal mechanism to finger individuation may be relatively small. The peripheral reason for the relatively smaller enslaving during finger flexion may include the extensor mechanism, which produces an extension action at the distal interphalangeal joint due to a structure of passive connective tissues (Li, Zatsiorsky et al. 2001). Furthermore, it has been reported that the forces in the action of the extensor mechanism reduce the intrinsic hand muscles and bone contact force at the metacarpophalangeal joint (MCP) (Hu, Howard et al. 2014) which may give rise to a positive effect on independent movements of individual fingers. One of the central reasons may be a consequence of a greater corticospinal projection ratio to the finger flexor muscles (Chye, Nosaka et al. 2010).

3.5.2. Multi-finger synergies in force and mode spaces

As we have already discussed, a higher enslaving during extension implies that fingers act less independently, which is accompanied by a relatively larger unintended force production. Furthermore, by comparison with the synergy indices (ΔV) in the force and mode space analyses, the synergy indices for the force stabilization during the steady state force production was larger during finger extension than during finger flexion, while the two space analyses were not statistically different (see Results 3.3.3 & 3.3.4). These results suggested that finger forces were coupled relatively stronger during finger extension by the abovementioned factors (i.e., peripheral and central), while hypothetical commands (i.e., finger force mode) to the fingers showed a stronger negative covariation (i.e., larger positive ΔV) during finger extension compared to finger flexion. Indeed, corticomotor excitability was affected by the directional constraints of movements (McMillan, Ivry et al. 2006) and was relatively larger for the extensor muscles than for the flexor muscle (Palmer and Ashby 1992). As such the findings suggested that corticomotor excitation is assumed to be purposeful actions for the planned movements, and could combine with the fact that a stronger co-variation between neural commands during finger extension in this study. The interdependency among finger actions leads to positive correlations between finger forces even though commands to finger (i.e., mode) are independent. The stabilization of the performance variable (i.e., total force) is generally achieved by negative co-variation between individual finger forces. In other words, the negative co-variation between elements (e.g., forces or modes) is a typical strategy to compensate performance errors elicited by elements resulting in stable net force production. Thus, a strong interdependency of finger actions contributes to the positive relationship among finger actions, which increases the demand for a proper co-variation (i.e., error compensation) among the fingers for a stable total force production.

In addition, there were two distinctive characteristics of the time profile of the net forces and stability indices during finger flexion and extension. First, the time to produce a quick pulse force was faster and consistent when the pulse force direction was opposite to the direction of the steady-state force (EF & FE conditions. see Result). Note that gravity is not an issue when interpreting the result because the experimental frame in this study was vertically oriented so that the finger flexion and extension forces were gravity-free measures. It is well known that electromechanical delay (i.e., EMD, the delay between an electrical state in the muscles and a mechanical action within the human body (Corcos, Gottlieb et al. 1992)) is shorter during eccentric muscle contraction (Cavanagh and Komi 1979). Eccentric contraction can be observed where a counter-movement occurs prior to a primary movement (Komi and Bosco 1978). The shorter and consistent force production in the FE and EF conditions could be associated with shorter electromechanical delay (EMD). The other distinctive observation is that the decreased in the magnitude of stability ($\Delta\Delta V_{peak}$) indices during a quick change in total force was larger in the conditions of FF (flexion to flexion) and FE (flexion to extension) compared to the conditions for EE (extension to extension) and EF (extension to flexion) in both the force and mode space analyses. In other words, the level of destabilization for a quick change in the overall performance may depend on the direction of the force before the rapid change and not the force direction intended for the quick change. It seems that the decreased in the magnitudes of the stability indices rely on the history of the finger force direction for stable force production and not on the direction of future actions. Thus, the immediate history-dependent changes of stability indices may be associated with neuromuscular hysteresis (Partridge 1965, Joyce, Rack et al. 1969, Gielen and Houk 1984).

3.5.3. Anticipatory synergy adjustment

The human control system, the central nervous system (CNS), is capable of changing the stability properties of the performance in advance or capable of changing the performance directly against a predictable perturbation (Kim, Shim et al. 2006, Shim, Park et al. 2006, Olafsdottir, Kim et al. 2008, Wang, Watanabe et al. 2016). Notably, the predictable perturbation should induce a mechanical effect resulting in changes in the salient performance variables. In the human movement system, there are two different, but complementary, types of feedforward movement control, and those are anticipatory synergy adjustment (ASA) and anticipatory postural adjustment (APA). The main observation when implementing ASA is the destabilization of the system (i.e., a decrease in the synergy index) against a predictable change in a salient performance variable, which has been well documented by previous studies (Klous, Mikulic et al. 2011, Sousa, Silva et al. 2015, Piscitelli, Falaki et al. 2017). In a redundant system, the destabilization, which could be achieved by the change in the co-variation pattern of the elements, could result in close to zero net mechanical effect due to extra degrees of freedom (DOF) with respect to the DOFs of the tasks. Therefore, ASA as a feedforward adjustment used by the CNS adjusts the synergy parameters (i.e., stability properties) without obvious changes in the net performance. In contrast, APA emphasizes changes in the performance variables such as muscle activations and the net force/moment prior to the upcoming perturbation. Previous experiments have shown that APAs were observed in average muscle activation patterns in a time series and that APA induces changes in the salient performance variables (Cavanagh and Komi 1979, Patla 2004, Sousa, Silva et al. 2015). In particular, APA is observed after the occurrence of ASA in regard to its timing. The function and timing of APA and ASA are different, but it has been assumed that a single or similar neural mechanism has a role in both phenomena.

Earlier studies reported parallel changes in the synergy indices and ASA with various populations and treatments including aged-group (Kapur, Zatsiorsky et al. 2010, Wang, Watanabe et al. 2016), Parkinson's disease patients (Bleuse, Cassim et al. 2008, Jacobs, Lou et al. 2009, Park, Wu et al. 2012, Park, Lewis et al. 2014, Sousa, Silva et al. 2015), patients with the cerebellar disorder (Park, Lewis et al. 2013), and effect of vibration on the intrinsic hand muscles (Arpinar-Avsar, Park et al. 2013). Another group of studies have reported non-parallel changes in synergy indices and ASAs. Cortical stroke survival showed the delayed ASA but no difference in the strength of synergy as compared to the control subjects (Cho, Min et al. 2010). Additionally, the synergy indices and muscular strength increased with wrist strength-training (Park, Han et al. 2015) while there was no difference in ASAs after the training (Partridge 1965). These two groups of studies have suggested that the subcortical structure including the cortico-basal-thalamocortical circuit has a critical role in both the formation and adjustment of the stability properties for the successful completion of tasks. Furthermore, it seems that the neural mechanism of ASAs may not be affected by the strength of the peripheries, which was also shown by no difference in ASAs between men vs. women (Shim, Lay et al. 2004). The results of this study suggest that the mechanism of ASAs may be strength- and direction-independent quantity and the neural process of feedforward adjustment could be a separate process controlling the co-variation between the elements.

Chapter 4. Effect of Frequency: Brain Oxygenation Magnitude and Mechanical Outcomes during Multi-Digit Rhythmic Rotation Task

4.1. Abstract

Feedback and feedforward controls have emerged as two important components in motor control theory to establish computational models and interpret experimental phenomenon. Recently, these two types of control strategies were supposed to be merged in both theoretic modeling and experimental observation. The integration of two controls was affected by movement property like speed/frequency. However, the mechanism of the integration, especially the function of brain regions in coordination of mechanical outcomes, is still under investigation. The current study measured regional brain oxygenation magnitude using PET, forces and moments performed by digits during multi−digit rotation task in two frequency conditions. Coordination of mechanical outcomes was calculated based on uncontrolled manifold (UCM) approach. According to the opposite correlations between brain oxygenation magnitude and mechanical outcomes in two conditions, two sets of brain regions were identified which showed involvements of feedforward and feedback motor controls respectively. The function of feedback control was verified to be reducing task−satisfied variability associated with activation in sensory cortices. In contrast, the function of feed−forward control was relevant with the perception of task goal and predictive motor planning involving prefrontal, limbic and subcortical areas. Furthermore, the effect of task difficulty based on movement frequency was discussed on the relative contributions of feedforward and feedback controls.

4.2. Introduction

Over the last century, numerous models have been proposed to describe the generation of human movement by motor system and its relationship with the activity of the central nervous system (CNS). Among those, feedback and feedforward controls have emerged as two important components in motor control theory to establish computational models and interpret experimental phenomenon. Classically, feedback control represents the process of regulating the input of the motor system (i.e. motor command from the CNS) based on the output of the system (i.e. sensation includes visual, auditory, somatic, and other sensory information, which always be delayed deal with the time for command execution and signal conduction) (Stanley 1981, Jordan and Wolpert 1999). Oppositely, feedforward control is considered as the process that the CNS can generate predictive motor command to perform the desired action based on prior perception and without regard to the consequences of the action (Grüsser 1995, Wolpert and Kawato 1998, Kawato 1999). Therefore, both functions of feedback and feedforward controls are implemented based on neural activity and reflecting to the motor performance. Motor control theorists and experimentalists have made either-or arguments about feedforward and feedback controls for many years. In modern models, the two types of control strategies were supposed to be merged to generate accurate movement which also be applied to the design of humanoid robots (Kuo 2002, Haeufle, Grimmer et al. 2012, Hong, Oh et al. 2013, Haeufle, Schmortte et al. 2018). Besides, the experimental observations also confirmed the combination of feedback correlation and predictive feedforward adaptation during movement such as walking, reaching and finger tapping (Wolff, Kotwica et al. 1998, Desmurget and Grafton 2000, Bove, Tacchino et al. 2007, Höhne, Stark et al. 2011). Moreover, the combination of those two controls were demonstrated to be adjustable affected by physical development (Wolff, Kotwica et al. 1998, Hay and Redon 1999) and movement features such as movement speed and task complexity (Bove, Tacchino et al. 2007). Take movement speed for instance, previous studies have demonstrated less adaptation relied on feedback during rapid movement compared to slow movement (Hay and Bard 1984, Beaubaton and Hay 1986, Messier, Adamovich et al. 2003, Yang, Leung et al. 2014). These evidences developed the utilization of movement speed in investigating motor control mechanism. Recently, the investigation about the functions of feedback and feedforward controls were developed from behaviors level to muscle activation and further to spinal cord or cerebellum (Morton and Bastian 2006, Gordon, Wu et al. 2010, Müller, Häufle et al. 2015). However, few is known about the contribution of brain activation to the accomplishment of those two controls, especially their integration. As the origin of motor command, the function of brain activation may be the ultimate item to improve the understanding of motor control mechanism, the application in diagnosis and rehabilitation on neural diseases, as well as the development of brain-computer interface devices assisting movement functions. Relevantly, the current study was proposed to investigate the interaction of feedback and feedforward controls in sights of both brain activation and behavior during multi-digit rotation action with different speeds (i.e., frequencies).

Multi-digit rotation action is a complex action accomplished under the satisfaction of several mechanical constraints (i.e., required conditions) on the mechanical outcomes of the digits. The number of elements (i.e., mechanical outcomes) is larger than constraints (see details in Method) which composing a redundant motor system and the problem of degree of freedom (DOF) (Bernstein 1967). Recently, the idea of uncontrolled manifold (UCM) approach has been applied to investigate the control strategy of the redundant motor system in humans (Latash 2000). The changes of elements were separated into the variance doesn't affects the performance error (uncontrolled manifold, V_{UCM}) and the variance does (controlled or orthogonal manifold, V_{ORT}). For instance, the reduced performance accuracy in the absent of visual feedback information represents the decreased of V_{ORT} (Slifkin, Vaillancourt et al. 2000, Vaillancourt and Russell 2002, Shapkova, Shapkova et al. 2008, Ambike, Zatsiorsky et al. 2015). Synergy index was defined as the difference between V_{UCM} and V_{ORT} normalized to the total variance per DOF as an index estimating performance stability (Scholz, Kang et al. 2003). Previous studies have demonstrated the predictive changes of synergy index in preparation of quick actions which is widely known as a feedforward control, anticipatory synergy adjustment (ASA) (Klous, Mikulic et al. 2011, Zhou, Wu et al. 2013, Park and Xu 2017). Furthermore, the occurrence time and amplitude of ASA affected by neurological disorders such as Parkinson’s diseases and cortical stroke (Park, Wu et al. 2012, Jo, Park et al. 2015, Latash and Huang 2015, Jo, Maenza et al. 2016). These studies suggested brain functioned as an essential role in the adjustment of synergy index and further in the feedback and feedforward controls. Therefore, the current study was proposed to investigate the two controls via the relationship in brain activation and synergy adjustment.

The investigating of brain activation involved in voluntary movement has penetrated onto operational (e.g., metabolic, hemodynamic) features, profiting from the development of neuroimaging technologies such as functional magnetic resonance imaging (fMRI) and positron−emission−tomography (PET). The blood oxygen related variables (e.g. regional cerebral blood flow, rCBF) elicited from fMRI and PET were considered as effective variables to describe animal or human brain activations in specified regions (Colebatch, Deiber et al. 1991, Jueptner and Weiller 1995, Sadato, Ibañez et al. 1997). Naturally, studies about regional rCBF during movement targeted from motor cortex to the surrounding cortical areas and further to subcortical structures by comparing movements with different speed/frequencies (Sadato, Ibañez et al. 1997, Kuboyama, Nabetani et al. 2005), complexities (Sadato, Campbell et al. 1996), or by comparing movement in people with/without special neural diseases/damage (Stoodley and Schmahmann 2009, de Abreu, Teodoro et al. 2018). However, back to the idea of Jackson, J. H. in the 1870s, the functions of a number of brain regions have been considered as involved in the motor control of a single body part like hand (Jackson 1873). Modern subdivision of the brain regions is supposed to establish a reliable brain atlas allow distinctly defining of anatomically and functionally structures and mapping their functions and connections (Fan, Li et al. 2016). Therefore, the measurement of brain activation in larger-scale, instead of specified regions, is more effective to verify the connections among regions and the functions of the connections in motor control. By measuring large-scale brain activation, several studies demonstrated activation of brain regions showed opposite relationship with movement property such as difficulty (Seidler, Noll et al. 2004), endpoint speed (Shirinbayan, Dreyer et al. 2019). However, since most measurements of large-scale brain imaging are taken restrained in a scanner, the measured movements were those with scarce body movement such as eye movement, and simple finger movement like reaching and finger tapping. Oppositely, the current study was proposed to investigate the coordination of elements during complex movement like multi-digit rotation and regional brain functions in feedforward and feedback controls through large-scale brain imaging using PET.

In summary, the current study measured the brain imaging using PET and mechanical outcomes performed by digits during multi-digit rotation tasks under two frequency conditions. It is expected to detect correlations between regional brain activations and mechanical outcomes including synergy indices. However, the correlations in specified brain regions were supposed to be affected by rotation frequency. This study discussed the functions of brain regions in terms of how are they employed in the processes of feed-forward and feedback controls. It might be the prior knowledge for more comprehensive motor control theory and applications in the fields of robotics and clinical medicine about brain damage.

4.3. Method

4.3.1. Subjects

Eight right-hand dominant young males (age 30.3 ± 2.7 years, height 175.8 ± 6.8m, weight 72.4 ± 10.0 kg) volunteered to participate in the study. All the subjects were answered negatively for previous history of neurological disorders and upper extremity injury including forearm, hand, and fingers. All the subjects were informed the consent approved by the Institutional Review Board (IRB) at Seoul National University (IRB No. 1705/003-013).

4.3.2. Apparatus

Three six-component force transducers (Nano-17, ATI Industrial Automation, Garner, NC, USA) were used to measure forces of three axes produced by thumb, index, and middle finger tips of the left hand. The sensors (size ϕ17mm × 14.5mm) were attached to a vertically oriented customized flat aluminum plane (size 74 mm × 19 mm × 5mm). One sensor was at the central of one side while other two sensors were ± 23.5 mm away from the central at the other side which composed the rotated handle (Figure 4-1C). Added weights, which had same shape and weight with the sensors, were attached to the counter side of the handle for each sensor. In addition, customized aluminum tablets were attached to both top and bottom of the handle horizontally with same weight. In other words, the center of mass of the handle was balanced at the center of the vertically oriented plane. Each sensor was covered with sandpaper (300-grit) to increase the friction between the finger-tips and the top surface of the sensors. Finally, the total weight of the handle was 290 ± 4 g. The force signals were digitized at 100 HZ using a customized Labview (National Instruments, Austin, TX, USA) program.

Three infrared reflective markers (diameter 4 mm) were attached to the lateral side of the vertically oriented plane. One marker was at the central while the other two were ± 25 mm away from the central (Figure 4-1C). The real-time positions of these three markers were showed on the feedback screen (24-inch, 1920 × 1080 resolution at 60 HZ) positioned at eye level (Figure 4-1B). A set of frames in the screen indicated the required space of the markers' moving, which represented the posture of the handle in the vertical space, that was restricting the handle rotate between ± 45 degree with the movement of the center less than 20 mm. Above the feedback of positions, a slider moved back and forth to remind the required speed. In addition, other three markers were attached to the top of the handle located as a right angle to measure the posture of the handle in the horizontal space (Figure 4-1C). The positions of all markers were measured by motion capture system with four cameras (Optitrack, NaturalPoint, Corvallis, OR, USA) (Figure 4-1A).

Subjects wore a paired of deluxe prism glasses to receive all the feedback while lying to take 18F-fludeoxyglucose (FDG) PET scan (Figure 4-1A). PET images were collected using PET/CT system Discovery-600 (D-600, GEMS, Milwaukee, WI). The dosage of FDG was 3 megabecquerels per kilogram of body weight for each scan. The left hand was in the air to rotate the handle while the forearm was supported and held stationary with Velcro straps.

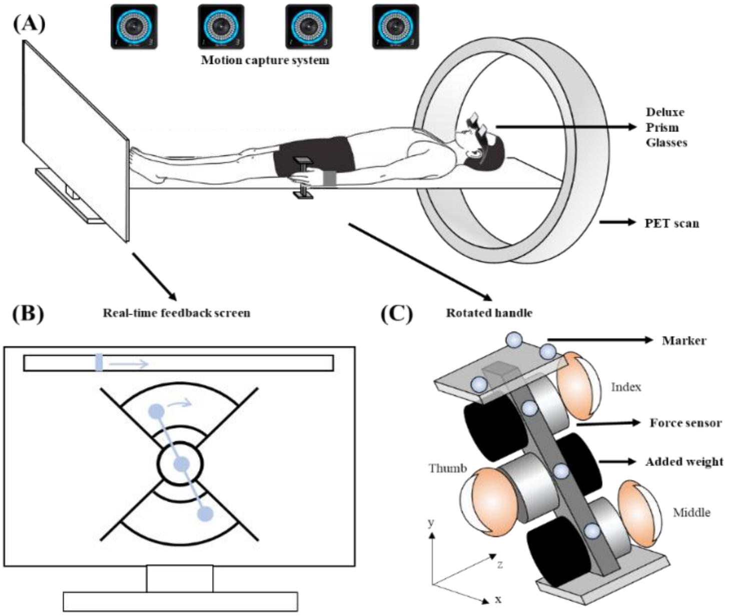

Figure 4-1: Illustration of experimental setup in multi-digit rhythmic rotation task.

Illustration of experimental setup. A) The subjects lied on the PET scanner, wore a paired of deluxe prism glasses, and hold a customized rotated handle. B) The feedback screen displayed the real-time posture of the handle and a slipper metronome. C) Three force sensors were attached to a vertically oriented aluminum plane.

4.3.3. Procedures

The main experiment was taking PET scan while performing a costumed rotation action which was grasping the rotated handle with thumb, index, and middle finger of left hand above the three sensors and rotating the handle in the y−z space only using the three fingers of left hand (Figure 4−1C). The requirement of the rotation action was moving the positions of the markers in the required space, both of which were shown in the feedback screen (Figure 4−1B). Before the experiment, subjects practiced the rotation action for 15−20 min under the same setup but without PET scan. After the practice, all subjects can do the rotation action successfully in both slow and fast rotation tasks.

Each subject took PET scan three times: 1) baseline scans, 2) slow condition, and 3) fast condition. In the baseline scans, subjects were instructed to lie on the scanner without any action for 50 min. The slow and fast conditions also took 50 min which consisted of 5 min rest, three blocks of combination of 100 s test and 100 s rest, 10 min rest, other three blocks of combination of 100 s test and 100 s rest, 15 min rest in sequence. Only the action of left hand was allowed in the slow and fast conditions. Subjects were required to do rotation actions during every 100 s test blocks. Subjects can pause the rotation action anytime to adjust grasping posture under the help of experimenter. The frequency of slipper metronome, which represented the required speed of rotation, was 0.15 HZ in the slow rotation tasks and 2.15 HZ in the fast rotation tasks.

4.3.4. Data Analysis

- PET imaging data

PET imaging data was analyzed using Patlak plot (Patlak and Blasberg 1985) which is a graphical method based on the compartment model that uses linear regression to identify and analyze pharmacokinetics of tracers involving irreversible uptake, such as deoxyglucose in this case. The compartment model in the current study was a two−compartments model including the central compartment where the deoxyglucose was in rapid equilibrium with plasma and the peripheral compartment where the deoxyglucose entered without ever leaving.

The net uptake rate for FDG (K) was calculated using the equation below:

$$\frac{R(t)}{C_p(t)} = K\frac{\int_0^t C_p(\tau)}{C_p(t)} + V_0,$$

where R represents the amount of deoxyglucose in region of interest; C_p represents the concentration of deoxyglucose in plasma; V0 represents the distribution volume of deoxyglucose in the central compartment. The R and C_p were measured by PET device while the unknown constants K and V_0 were calculated by linear regression. The regions of interest in the current study were 50 regions of the brain separated according to the Brainnetome Atlas (Fan, Li et al. 2016), including 24 regions in the left hemisphere, corresponding regions in the right hemisphere, and 2 regions in the cerebellum (more details in the results). For each subject and each region of interest, calculated ΔK_{slow} and ΔK_{fast} represent the changes of K in the slow and fast conditions respectively comparing with the baseline scan.

- Finger force data

Customized MATLAB (MathWorks Inc., Natick, MA, USA) codes were written to process the measured force data. Before variable computation, the raw signals were digitally low-pass filtered at 10 Hz cut-off with zero-lag, 4th-order Butterworth filter.

Virtual finger (VF) forces and moments were calculated as the vector sum of individual finger (IF, i.e. index and middle fingers) forces and moments. A hierarchical control of the CNS based on the concept of VF has been suggested as a possible strategy to generate a desired task performance (MacKenzie and Iberall 1994, Baud-Bovy and Soechting 2001). Note that the action of the VF can be the same as mechanical effects produced by IF. The analysis was performed both at the VF level and IF level.

According to the requirement, the following three dynamic constraints (i.e., mechanical constraints) existed during the task regarding thumb and VF forces and moments in the vertical x−y plane.

Normal force constraint:

$$F_n^{th}(t)+F_n^{vf}(t)=0,\ F_n^{vf}(t)=F_n^{i}(t)+F_n^{m}(t);$$

Tangential force constraint:

$$F_t^{th}(t)+F_t^{vf}(t)=G,\ F_t^{vf}(t)=F_t^{i}(t)+F_t^{m}(t);$$

Moment of force constraint:

$$M_n^{vf}(t)+M_t^{th}(t)+M_t^{vf}(t)=I\alpha(t),$$

$$M_n^{vf}(t)=F_n^{vf}(t)\cdot D^{vf};$$

where subscript n and t refer to the normal and tangential force components; superscripts th , vf, i and m refer to thumb, VF, index and middle fingers; M represents the moment of forces respect to the center of the handle (which means the moment of F_n^{th} was zero); D represents the moment arm of normal forces; d represent the moment arm of tangential forces which is a constant as the width of the handle; G, I and α represent the gravity, moment of inertia and angular acceleration in the x−y plane, respectively.

The forces and moments above are functions respect to the effective time of the rotation action which was out of 100s test period except time to adjust grasping posture in six blocks. In both slow and fast conditions, the average forces, moments and moment arms across action time during each block were calculated as mechanical outcomes to test the formulated hypotheses.

- UCM analysis

The co−variation of finger forces (i.e. multi−finger synergy), was quantified based on the UCM approach (Scholz and Schöner 1999, Latash, Scholz et al. 2002, Scholz, Kang et al. 2003) using the time series of force data for each block, condition and subject. UCM analysis were applied in both normal and tangential directions at the VF level because task requirements were occurred between thumb and VF forces and moments. For instance, variance of thumb and VF normal forces in uncontrolled manifold (V_{ucm}^{n}) means simultaneous increase or decrease of these two normal forces which doesn't affect the satisfaction of normal force constraint while variance of thumb and VF tangential forces in orthogonal manifold (V^t_{ort}) means simultaneous increase or decrease of these two tangential forces which affects the satisfaction of tangential force constraint. Synergy indices (ΔV^n and ΔV^t) were quantified as the relative amount of V_{UCM} in the sum of V_{UCM} and V_{ORT}.

- Correlation between neural activation and mechanics

Pearson correlation between calculated mechanical variables (i.e. forces, moments, moment arms, V_{UCM}, V_{ORT}, and ΔV) and imaging variables (i.e. ΔK in all regions) across all subjects were analyzed in two frequency conditions. Correlation coefficient with an absolute value larger than 0.7 was considered as one mechanical variable be significantly correlate with the neural activation in one region.

- Statistics

Statistical non-parametric mapping (SnPM) was applied to compare brain imaging results inter-condition and find the regions in which there were significantly different activities between two conditions. It is an effective method for the multiple comparisons problem implicit in the standard voxel-by-voxel hypothesis testing framework and analyzing multi-subject PET or fMRI designs assessed for population effect. The significantly level for SnPM was set as $p < 0.01$.

The comparisons of calculated mechanical variables between two frequency conditions were conducted using one-way repeated measures ANOVA with factors conditions (slow and fast). Mauchly's sphericity test was employed to confirm or reject the assumptions of sphericity. The significantly level for ANOVA was set as $p < 0.05$.

4.4. Results

4.4.1. PET imaging

No difference between left and right hemispheres in all three conditions. Some regions were found with significant ($p < 0.01$)

increases of K in slow and fast conditions compared with baseline condition such as visual cortex, right motor cortex (PrG by the subdivision in the current study), and thalamus (Figure 4−2). Wider regions showed increased K in slow condition than in fast condition.

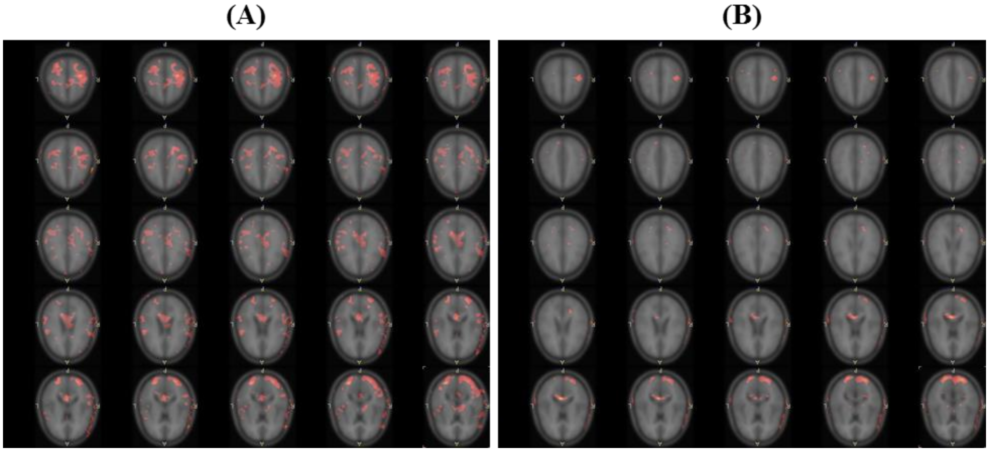

Figure 4−2: The results of SnPM analysis for PET measurement.

The results of SnPM analysis for PET measurement. The regions highlighted by red represent significantly increased K in (A) slow or (B) fast conditions compared with baseline condition. Rows from up to down represent layers of the brain from top to bottom. Columns were samples of subjects.

4.4.2. Finger forces

At the VF level, the normal forces of thumb and VF (F_n^{th} and F_n^{vf}) was significantly larger in the fast condition than in the slow condition ($p < 0.05$) (Figure 4−3A). The average of F_n^{th} and F_n^{vf} across subject were 7.78 N and 7.75 N in the slow condition while 11.76 N and 11.71 N in the fast condition, respectively. Oppositely, there were no significant differences between two conditions for both tangential forces of thumb and VF (F_t^{th} and F_t^{vf}) ($p > 0.05$). The average of F_t^{th} and F_t^{vf} across subject were 1.52 N and 1.45 N in the slow condition while 1.49 N and 1.40 N in the fast condition, respectively. Comparison of forces at the IF level were in consistent with the VF level which showed significant increases of index and middle finger normal forces (F_n^i and F_n^m) ($p < 0.05$) but not tangential forces (F_t^i and F_t^m) ($p > 0.05$) in the fast condition than in the slow condition. No significant difference ($p > 0.05$) was found in moment (M_n^{vf}) and moment arm (D^{vf}) at the VF level (Figure 4–3B). At the IF level, moments of index and middle finger normal forces (M_n^i and M_n^m) significantly increased ($p < 0.05$) in the fast condition than in the slow condition. Whereas, there was no significant difference in moment arms of index and middle finger normal forces (D^i and D^m) ($p > 0.05$))

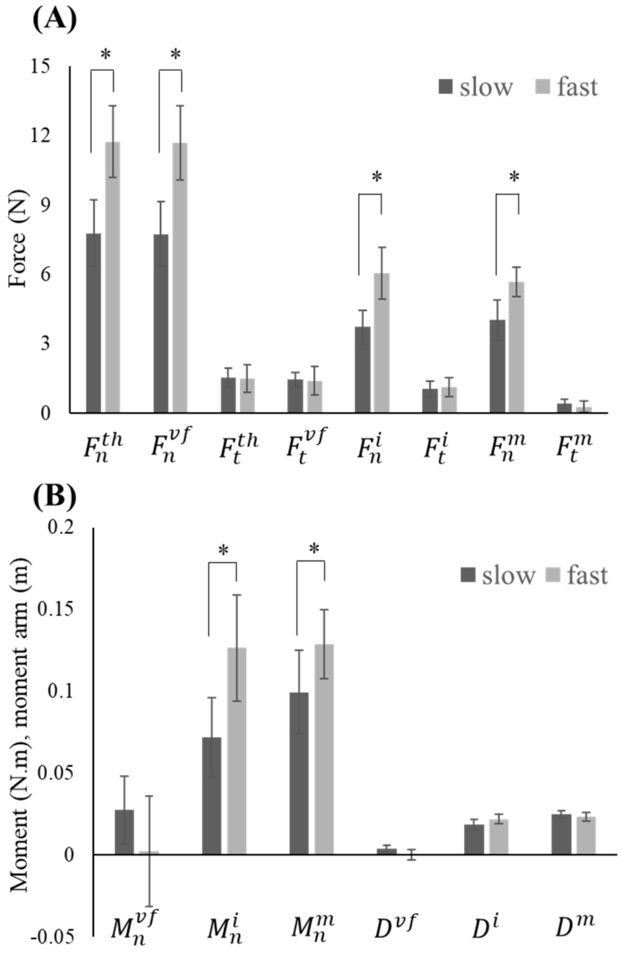

Figure 4–3: Magnitudes of mechanical outcomes.

Magnitudes of mechanical outcomes including (A) F_n^{th}, F_n^{vf}, F_t^{th}, F_t^{vf}, F_n^i, F_t^i, F_n^m, F_t^m and (B) M_n^{vf}, M_n^i, M_n^m, D^{vf}, D^i, D^m averaged across subject in slow (black bars) and fast (gray bars) conditions. F, M and D refer to the forces, moments and moment arms;

subscript n and t refer to the normal and tangential force components; superscripts th, vf, i and m refer to thumb, VF, index and middle fingers. The asterisks (*) show significant differences between conditions ($p < 0.05$).

4.4.3. UCM analysis

Variance of thumb and VF normal forces in uncontrolled manifold (V^n_{ucm}) was significantly increased ($p < 0.05$) in the fast condition than in the slow condition while variances in orthogonal manifold (V^n_{ort}) was similar in two conditions ($p > 0.05$) (Figure 4-4). As the relative amount of V^n_{ucm}, synergy index (ΔV^n) was also larger in the fast condition ($p < 0.05$). In contract, no difference was found in UCM variables for tangential forces (V^t_{ucm}, V^t_{ort}, and ΔV^t) ($p > 0.05$).

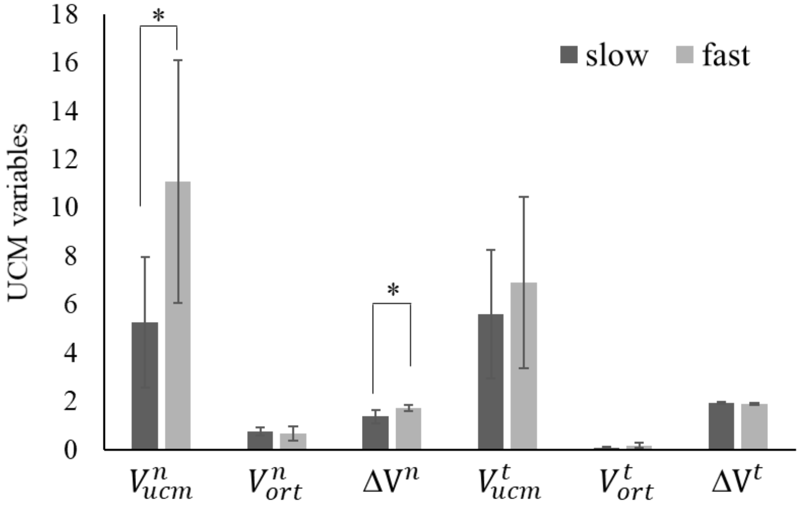

Figure 4-4: UCM variables including V_{ucm}, V_{ort}, and ΔV for normal and tangential forces.

UCM variables including V_{ucm}, V_{ort}, and ΔV for normal and tangential forces averaged across subject in slow (black bars) and fast (gray bars) conditions. The asterisks (*) show significant differences between two conditions ($p < 0.05$).

4.4.4. Correlation between neural activation and mechanics

Mechanical variables at both VF level and IF level and UCM variables showed significant (|r| > 0.7) correlations with neural activations in some regions in two conditions. In the slow condition, there were wide regions correlated with mechanical variables including F_n^{th} (6 regions), F_n^{vf} (4 regions), F_t^{vf} (3 regions), F_n^i (2 regions), F_n^m (12 regions), F_t^i (11 regions), M_n^{vf} (10 regions) , M_n^i (2 regions) , M_n^m (20 regions), D^{vf} (2 regions), D^i (1 region), D^m (1 region). In the fast condition, comparing to the slow condition, different mechanical variables showed correlations with neural activations in different regions which were F_n^{th} (2 regions), F_n^{vf} (2 regions), F_t^{th} (1 region), F_t^{vf} (14 regions), F_n^i (1 region), F_n^m (2 regions), F_t^i (9 regions), F_t^m (1 region), M_n^{vf} (2 regions) , M_n^m (8 regions), D^{vf} (2 regions), D^i (14 region), D^m (10 region). In contrast, UCM variables showed significant (|r| > 0.7) correlations with neural activations in wide regions (35 regions) in the slow condition while little region (6 regions) in the fast condition. Besides, there were wider regions correlated with V_{ucm}^n (30 regions) and ΔV^n (11 regions) than V_{ucm}^t (4 regions) and V_{ort}^n (3 regions) in the slow condition. No significant correlation was found between neural activations in all regions and other UCM variables including V_{ort}^n and ΔV^t . Figure 4-5 shows the number of mechanical variables significantly correlated brain activation in each region. More correlations were demonstrated in the temporal and occipital lobes in the slow condition while more correlations in the frontal lobe and subcortex in the fast condition.

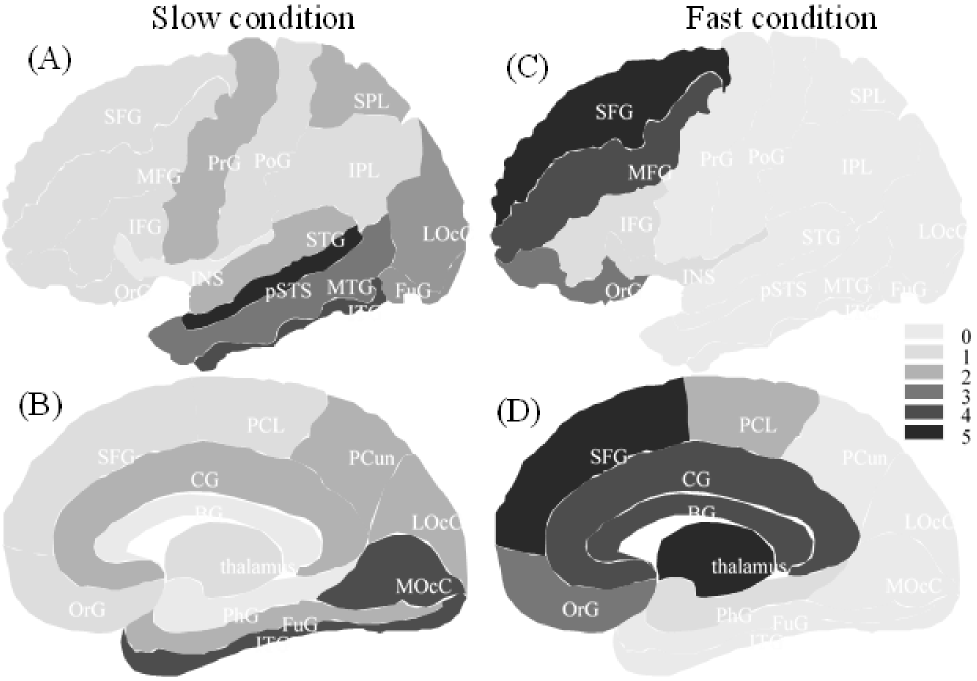

Figure 4-5: Number of mechanical variables showed significant correlation with brain activity.

Number of mechanical variables showed significant correlation with brain activity. Regions have more correlated variables displayed in deeper color. Both cortical level (A) and sub-cortical level (B) in the slow condition were showed in the left while cortical level (C) and sub-cortical level (D) in the fast condition were showed in the right.

4.5. Discussion

The results revealed inter-condition differences in correlations between mechanical outcomes and brain activations based on regional cerebral blood flow measurement. Two sets of brain regions were detected based on the differences of correlations across rotation frequencies. The 1st set of brain regions including most parts of the occipital, parietal and temporal lobes, showed activations correlated with multiple mechanical outcomes during slow rotation action but not fast rotation action. Oppositely, in the 2nd set, correlations were detected during fast rotation action but not slow rotation action. These regions included the frontal lobe, especially the prefrontal lobe (i.e., including SFG, MFG, IFG, and OrG by the subdivision in the current study), the limbic Lobe (i.e., CG) and parts of subcortical nucleus (i.e., basal ganglion, and thalamus). It implied synchronized adjustments of these two sets of brain regions depending on movement frequency. Note that the brain wasn't supposed to be divided into two isolated parts. Instead, these two parts activated and contributed to motor control differently across movement frequencies.

4.5.1. Regions involved in feedback

The 1st set of regions (i.e., most parts of the occipital, parietal and temporal lobes) are supposed to be involved in the process of sensory information. The 1st set of regions include those connecting with peripheral neurons and receiving sensory information from peripheral receptors. For instance, visual sensations from the retina carried by the optic nerve travel through optic chiasm to the lateral geniculate body of the thalamus and terminate in the occipital lobe (Freud, Plaut et al. 2016, Joukal 2017, Xie, Fan et al. 2019). Somatosensory, concerned with tactile sensation and proprioception, ascends through the spinal cord and a decussation in the midbrain, then arrives a thalamic nucleus and finally terminates in the parietal lobe (Barrett, Barman et al. 2009, Mtui, Gruener et al. 2015). The auditory and vestibular information is also relayed to the cerebral cortex, usually considered as the superior temporal gyrus, STG which is also a higher order visual region (Oh, Boegle et al. 2017, Dieterich and Brandt 2018, Oh, Boegle et al. 2018). In addition, the corticocortical communication among these regions and motor cortex were demonstrated as a part of sensory processing pathways by measurements of animal brain (Iacoboni, Koski et al. 2001, Rizzolatti and Luppino 2001, Disbrow, Litinas et al. 2003, Zagha, Casale et al. 2013). As showed in the results, the neural activations in the occipital, parietal and temporal lobes were correlated with a number of mechanical outcomes during slow rotation action but oppositely bare variables during fast rotation action. It implied that these regions more actively communicated via neural pathways to process sensory information for the motor control during slow movement than fast movement. As introduced before, the process of sensory information is the foundation of feedback control. It suggests essential roles of the occipital, parietal and temporal lobes in the feedback control while the interposition of feedback control affects by the frequency of rhythmic movement.

What is the role of sensory information and what is controlled by feedback in the process of motor control? Traditionally, the use of sensory information from vision, auditory, and tactile sensations, is believed to reduce the performance error (Kluger and DeNisi 1996, Dennerlein, Martin et al. 2000, Cockburn, Quinn et al. 2011). However, the mechanism of feedback control is still unambiguous although various experiments and models have been applied to explore it (Scott 2004, Petryński 2010, Milton, Insperger et al. 2018). In the current study, performance error represents the difference between thumb and VF normal forces which causes unexpected horizontal movement of the handle. In the context of UCM hypothesis, performance error is consistent with the definition of orthogonal variance (Scholz and Schöner 1999). But out of the traditional thoughts, the results showed balanced normal forces and no inter-conditional difference in the value of orthogonal variances. It indicated that the process of sensory information was irrelevant with reducing performance error which was further confirmed by the barely correlated orthogonal variances and regional brain activations in both conditions. Therefore, the function determining performance error may be carried by neural system out of the cerebral cortices, such as midbrain or spinal cord. Previous experiments for spinal cord injury support this idea (Piantino, Burdick et al. 2006, Cramer, Orr et al. 2007, Mohandas Nair, George Hornby et al. 2012). Oppositely, with the interposition of feedback control during slow movement, UCM variance was reduced and correlated with the activations of a number of brain regions. It suggests the function of sensory feedback control associated with reducing the UCM variance which represents the flexible coordination among performance-related elements (Scholz and Schöner 1999). This consequence was consistent with previous observations of reduced UCM variance when removing sensory feedback in both hand and locomotion tasks for healthy or brain-diseased humans (Ranganathan and Newell 2008, Ranganathan and Newell 2009, Funato, Aoi et al. 2015, Jo, Ambike et al. 2016). Furthermore, previous study summarized the production of UCM variance, in other words, the implement of goal-equivalent variation, to be performed at a cortical level (Babikian, Kanso et al. 2017). For extending, the current study confirmed this idea and pointed its location excluding primary sensory cortices and prefrontal cortex since there was no correlation with UCM variance for these regions.

4.5.2 Regions involved in feedforward

In contrast, the 2nd set of regions (i.e., the prefrontal and limbic lobes, parts of subcortical nucleus) are supposed to be relevant with the task-related decision making and motor planning. Decision making in motor task colloquially refers to the organization of motor goal based on the prior instruction of the task and the observation of environment (Bandura and Wood 1989, Orasanu and Connolly 1993). It is a preparing process for the movement execution in a short-term future which generally be considered as encoded by prefrontal cortex (Manes, Sahakian et al. 2002, Barraclough, Conroy et al. 2004, Wallis 2007, Hare, Camerer et al. 2009). In the current study, brain activation in prefrontal cortex during fast rotation was correlated with normal forces and moment arms. These mechanical variables were highly consistent with those relevant with the task goal, rhythmic total moment changes with balanced normal forces. It indicated the outcome of decision making in the prefrontal cortex was passed to the motor system to be converted into following action which arguably matches the definition of motor planning. Recently, distinguishing from perceptional decision making, motor planning was considered as processes that reduce uncertainty about how the motor goal will be achieved by specifying the details of the following movement (Wong, Haith et al. 2015, Oostwoud Wijdenes, Ivry et al. 2016, Wong and Haith 2017). During fast movement in the current study, correlations of detailed mechanical outcomes including forces, moments, and moment arms were detected in limbic lobe and subcortical nucleus. It implied the location of motor planning in brain. In summary, the neural activity in the 2nd set of regions might be performed for the predictive implementation of the following movement according to prior knowledge and observation. This process is arguably consistent with the generation of predictive motor command in context of feed-forward model (Miall and Wolpert 1996, Wolpert and Kawato 1998). It suggests essential roles of the prefrontal, limbic lobes, and parts of subcortical nucleus in the feed-forward control and their significant contribution during fast movement.

What is the neural mechanism of the achievement of feed-forward control? The dynamics of neural activity were explored using the net population of neurons as a high-dimensional firing-rate space from large-scale neuron recording (Churchland, Cunningham et al. 2012, Kaufman, Churchland et al. 2013). During motor planning, the neural activity of cerebral cortex is regulated as converging to a low-dimensional subspace (Churchland, Byron et al. 2006, Kaufman, Churchland et al. 2013, Svoboda and Li 2018) which supports the concept of specifying desired movement and explains the correlation between preparatory neural activity and followed movement. Furthermore, preparatory neural activity was also detected in subcortex such as thalamus (Tanaka 2007) and cerebellum (Ohmae, Kunimatsu et al. 2017). It pointed multi-regional interactions involving subcortical areas relevant with feed-forward control. Note that the 2nd set of regions in the current study included not only prefrontal cortex but also cingulate gyrus, basal ganglia, and thalamus. Thalamus was proposed as processing both delayed sensory information to sensory cortices (Jones and

Powell 1970) and predictive information from the basal ganglia and cerebellum to motor cortices (Alexander, Crutcher et al. 1991, Houk and Wise 1995, Kurata 2005). And basal ganglia act to drive inhibition in the motor areas via thalamus and perform dimension reduction by evoking action potentials in interneurons (DeWolf and Eliasmith 2011). In addition, cingulate cortex is where the prefrontal cortex, thalamus, and basal ganglia interface (Paus 2001). In summary, a top-down circuit emerged among prefrontal lobe, limbic Lobe, basal ganglion, and thalamus which might implement the motor planning and communicate it with motor cortex. Coincidentally, this circuit supposed to be consistent with the circuits confirmed in predictive adaptation of heart rate or non-voluntary endocrinal actions which was traveling from the prefrontal cortex to the subcortical cortex through the cingulate cortex and arriving the spinal cord connecting with the endocrine (Dum, Levinthal et al. 2016, Eisenbarth, Chang et al. 2016). It confirms the existence of feed-forward network in the 2nd set of brain regions and implied its function of production without external inputs.

4.5.3 Corporation of feedforward and feedback

In summary, two sets of brain regions were identified which showed involvements of feedback and feed-forward motor controls respectively. The differences in correlations of two sets of brain regions in two experimental conditions indicated adaptable contributions of feed-forward and feedback controls. What dominates the adaptation of their contributions and brain activations in relevant regions? Previous studies also verified a relatively high contribution of feed-forward control in rapid movements even with confused sensing (Reader and Ehrsson 2019) which a relatively high contribution of feedback control in slow movement even with incorrect prior knowledge (Flannigan, Chua et al. 2016). Furthermore, the effect of some other variables was revealed in several studies such as target size and movement amplitude in reaching movement (Winstein, Grafton et al. 1997, Desmurget and

Grafton 2000, Seidler, Noll et al. 2004). The similarity among those variables is that all of them have been referred to as difficulty/complexity level of motor tasks. Task difficulty is an ambiguous concept encompassing a wide variety of classifications mostly according to a specify feature in behavior level (Campbell 1988). However, the regional differences of brain activation were confirmed in neural activity level in multiple motor tasks with different difficulty (Paus, Koski et al. 1998, Fournier, Wilson et al. 1999). In the current study, task difficulty based on frequency of rotation actions elicited the relative contribution of feedback and feed-forward motor control. Besides, reduced feedback control during fast rotation or more difficult task in the current study was associated with reduced UCM variance among elements. It implied the UCM variance, in other words, the flexible coordination among elements, might be a foundation to judge the difficulty of motor tasks in motor control level.

4.6 Conclusions

The current study investigated the blood oxygen related brain activations in anatomical regions and mechanical outcomes of fingers during multi-digit rhythmic rotation actions with different frequencies. Two sets of brain regions were identified showed involvements for feedforward and feedback motor controls respectively based on the correlations of brain activations in different regions with different mechanical variables. The movement frequency was suggested to affect the relative contributions of feedforward and feedback controls and further impact the coordination patterns of mechanical variables to satisfy task requirements. But limited by the PET technology, there was no time-sequenced brain activation data to confirm the processes in feedforward and feedback controls in each brain regions. Besides, the causation of inferences based on correlations may need confirmation using such as recording of brain signal production with direction information. At last, the measurements of neural activations in midbrain and spinal cord is necessary to investigate the error compensation and moreover the motor control in redundant human movement.

Chapter 5. Effect of Frequency: Brain Oxygenation Magnitude and Mechanical Outcomes during Multi-Digit Rhythmic Rotation Task

5.1. Abstract

Prefrontal cortex (PFC) has confirmed as an important role in motor control, which showed increments of oxygenation during motor adaptation or cognitive tasks. However, identical PFC oxygenation also be reported during rhythmic movements with different frequencies even though the performance was affected in the manner of speed-accuracy tradeoff (SAT). Therefore, it is unclear what is the neural mechanism of the influence caused by frequency during rhythmic movements, especially the contribution of cognitive process on motor control. This study measured the prefrontal cortex oxygenation during multi-digit rhythmic pressing actions with different frequencies. The correlations among digit forces and the prefrontal functional connectivity (FC) were computed. As results, both multi-digit correlation and FC in PFC decreased with movement frequency, as well as the performance as accuracy. These findings provide evident for the linkage between cognitive process and the generation of coordination during multi-digit human actions. Besides, the mechanism of SAT was suggested to be the selection of movement speed with relative changes in cognitive process.

5.2. Introduction

Benefit on the development of the approaches in neurophysiology such as functional near-infrared spectroscopy (fNIRS), scientists paid much more attention to investigate human motor control through measurement of neural activation in brain regions such as prefrontal cortex (PFC). PFC has confirmed as an important role in motor control. In structural, PFC has reciprocal connections with wide brain regions related to motor control, for example, basal ganglia, premotor cortex, supplementary motor area (see reviews in Fuster 2015 and Miller and Cummings 2017). In functional, PFC receives and processes information from sensory inputs and memory to form cognitive control in behavioral selection or planning as findings in mental tasks (see reviews in Miller and Cohen 2001 and Markowitz, Curtis et al. 2015). To further investigate the neural mechanism of motor control, previous studies recorded the activation of PFC and other brain regions in multiple movements. For instance, increments of PFC oxygenation were observed during motor adaptation such as changing from walking to running (Suzuki, Miyai et al. 2004) or suffering external perturbations against standing balance (Mihara, Miyai et al. 2008). These observations indicate the involvement of PFC and cognitive process in dynamic human movements.

Rhythmic movements of joints, segments or limbs are essential for human daily living and has developed into paradigms to investigate dynamic motor control and neural activation. For instance, during repetitive finger tapping tasks, the oxygenation in motor cortex increased with tapping frequency (Sadato, Ibañez et al. 1997, Agnew, Zeffiro et al. 2004, Kuboyama, Nabetani et al. 2005) which suggested a frequency-dependent motor control. However, only few studies showed that the frequency of rhythmic human movement doesn’t influence the ongoing PFC oxygenation (Jenkins, Passingham et al. 1997, Kim, Eliassen et al. 2005). Therefore, more evidences were required to verify the activation and function of PFC in dynamic motor control, especially in relation to the frequency of rhythmic movements. Recently, functional connectivity (FC) in PFC was widely applied to investigate the function of PFC in mental tasks. For instance, several studies reported reduced FC in PFC with increased task complexity (Lew, Rey et al. 2008, Maes, Swinnen et al. 2020, Mussini, Berchicci et al. 2020) and suggested the influence of cognitive process on FC in PFC (Rissman, Gazzaley et al. 2004, Wei, Yang et al. 2014, Clausen, Francisco et al. 2017). In this basis, both oxygenation and FC in PFC could be proposed to describe the cognitive process of motor control.

As a consequence of motor control, movement frequency negatively influences performance as reduced accuracy of motor outcomes comparing to the motor goal (Stegemöller, Simuni et al. 2009). This phenomenon is consistent with the well-known speed-accuracy tradeoff (SAT) stating that, the faster a movement, the less accurate it is, hence the higher the probability to miss the target (see reviews in Bogacz, Wagenmakers et al. 2010 and Heitz 2014). Differently, the SAT describes one single action while frequency influence acts in dynamic rhythmic movements. It is questionable whether the neural mechanism of these two negative influences are identical. In addition, movement frequency also influences the stability or variability of motor outcomes which estimated as the standard deviation either across trials or over samples of time series motor outcomes (Newell and Carlton 1988). For instance, gait studies revealed that trunk kinematic variability has the lowest magnitude at preferred speeds compared to lower and higher speeds (Dingwell and Marin 2006, Powell, Szekely et al. 2018). Higher frequency was associated with higher variability and more errors during repetitive assembly work (Bosch, Mathiassen et al. 2011) or multi-finger movements (Friedman, Varadhan et al. 2009). Specially, multi-finger variability reveals control of coordination among fingers to deal with the redundant system obtaining multiple degree of freedoms (DOFs) (Latash, Scholz et al. 2002). Therefore, the increase of movement frequency may modify the process of motor control and reduce variability among fingers during rhythmic multi-finger movements. Accordingly, the purpose of this study was to investigate the modified motor control associate with different frequencies in rhythmic multi-finger force production task. Besides, the oxygenation and FC of PFC were applied to investigate the function of PFC and cognitive process in motor control and relation to movement frequency.

5.3. Method

5.3.1. Subjects

Eight right−hand dominant young males (age 30.3 ± 2.7 years, height 167.49 ± 6.53 m, mass: 69.39 ± 15.73 kg) volunteered for to the current experiment. We confirmed that all the participants had no medical records of neurological disorders and upper extremity injury including forearm, hand, and fingers. Seoul National University Institutional Review Board (IRB) approved the use of customized experimental protocol related to multi−finger pressing tasks and compatible devices including a customized experimental frame, force transducers, and fNIRS device. All the experimental details were performed in accordance with the relevant guidelines and regulations. The consent was informed, and all the participants were requested to sign a consent form approved by the IRB at Seoul National University (IRB No. 2007/002−028).

5.3.2. Apparatus

Four force transducers (Nano−17, ATI Industrial Automation, Garner, NC) were attached to a customized experimental frame (140 × 90 × 5 mm), which measured individual finger forces about the z−axis (Figure 5−1A). The surfaces of transducers were covered with sandpapers to provide sufficient friction with fingertips. There were four slots in an anterio−posterior direction on the panel for adjusting the position of the transducers with the consideration of hand and finger size of individual participants. The mediolateral distance between two slots (i.e., two transducers) was 3.0 cm (Figure 5−1B). The experimental frame with the transducers was mechanically fixed on an immovable table. A total of four analogue signals from the transducers related to the normal force components were digitized with a 16−bit analogue–digital converters (USB−6225, National Instrument, Austin, TX) through a customized LabVIEW program (LabVIEW 8.0, National Instrument, Austin, TX). The sampling rate of force signals was set at 200 Hz. Before each trial, all signals from the transducers were zeroed.

Depth-dependent hemodynamic changes in the PFC were recorded using a wearable NIRST fNIRS device (NIRSIT, OBELAB, Seoul, Korea) at a sampling rate as 9 Hz. NIRSIT firm contacted on forehead to block the effect of ambient light which confirmed by the channel quality at an appropriate level (i.e., see for more details in Data processing section) before and during the experiments. The source-detector (SD) separation was 30mm as typical and there were 48 channels in total.

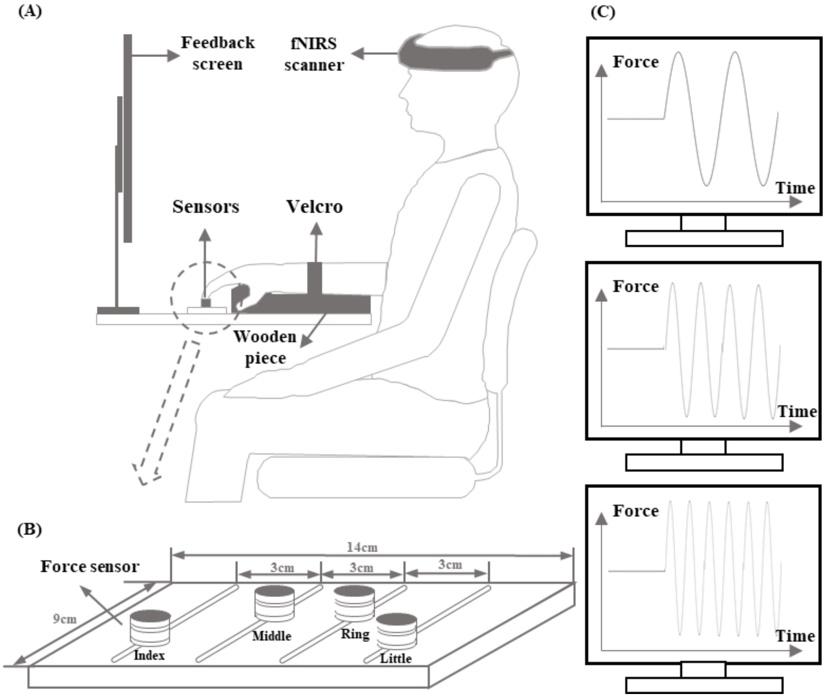

Figure 5-1: Illustration of the experimental setup in multi-digit rhythmic pressing task.

Illustration of the experimental setup (A). The subject's wrist was held stationary with Velcro straps. A wooden cylinder supported the palm, and the force sensors were attached to a frame (B). The feedback screen displayed the real-time finger forces and showed the templates combined by different sine waves during force production tasks (C).

5.3.3. Procedures

Participants sat in a height−adjustable chair pacing a computer screen. The forearm and positioned their right upper arm on a palm−forearm brace in order to ensure a constant configuration of hand and fingers during finger force production (Figure 5−1A). The forearm was held stationary with Velcro straps to prevent forearm and wrist movement, while the fingertips were placed on the centers of sensors. At the beginning, the maximal voluntary contraction (MVC) force using one individual finger or four fingers was measured for each participant and utilized in the setup of the ramp task and main task.

The ramp task was to estimate the effect of enslaving which described the nearly linear relations between changes in individual finger forces and in the total force during a multi−finger task (Latash, Scholz et al. 2002). In the ramp task, participants were asked to produce ramp pattern of one finger force from 5% to 25% of that finger's MVC in a duration of 6 s after maintaining 5% of that MVC for 2 s. Participants were instructed to focus on the force produced by the task finger and on the template displayed in the computer screen while ignoring the force produced by non−task fingers. Ramp tasks were performed twice for each of the four individual fingers with a 30 s rest between each two trial.

In the main task, participants were asked to produce total force of four fingers (F_{TOT}) following the template displayed in the rolling screen with the window length as 10 s (i.e. the displayed template ranged from 5 s prior to 5 s posterior to the current time). The force templates consisted of a 40 s steady force production (15% of MVC) followed by a 50 s cyclic force production which was a sinusoid with different frequencies and same amplitude (5% of MVC). There were three frequency conditions, force template conditions, including 1) 0.1 Hz as slow condition, 2) 1 Hz as middle condition, and 3) 2 Hz as fast condition (Fig. 5−1C). The 40 s steady state was designed to elicit a stable hemodynamic state before cyclic force production which utilized as a baseline in analyzing fNIRS imaging data (Bajaj, Drake et al. 2014). The 50 s cyclic state was designed to elicit several cycles for applying UCM analysis (i.e. see more details in 'Data analysis) without the effect of fatigue. Every participant had a 10–20 min practice until the performance index (i.e. see more details in 'Data processing') was less than 0.2 to ensure that the participant was able to perform the experimental tasks and remove the learning effect. After the orientation session and enough rest, each participant performed three trials with a 5 min rest between each two trials. Each trial consisted of three blocks in which the three frequency conditions were displayed in a random sequence with a 30 s rest between each two blocks.

5.3.4. Data Analysis

- Performance

Customized Matlab (Matlab 7.4.0, Mathworks, Inc) programs were written for force and fNIRS data analyses. For the force data analysis, individual finger forces (i.e. index finger force: F_i; middle finger force: F_m; ring finger force: F_r; little finger force: F_l) were digitally low–pass filtered with a 4th–order Butterworth filter at 10 Hz cut–off.

The time at the start of cyclic force production was defined as t0. Each cycle of the template during 10–40 s after t0 was separated into F_{DW} phase (i.e., from maximum to minimum) and F_{UP} phase (i.e., from minimum to maximum). Note that the number of cycles in each trial was different in conditions because of the different frequency and consistent duration (i.e., 3 cycles in slow, 30 cycles in middle, and 60 cycles in fast condition). For both F_{DW} and F_{UP} phases, the root mean square ($RMSE_{DW}$ and $RMSE_{UP}$) of F_{TOT} error (i.e. difference between measured F_{TOT} and the concurrent template force) was computed and normalized by the center level of target force (i.e., 15% of MVC). The average of

$RMSE_{DW}$ and $RMSE_{UP}$ across three trials was estimated as the performance for each frequency condition and participant.

- F−mode transformation

Changes in F_{TOT} at each sample of one cycle can be written as a function of the changes in individual finger forces, $\mathbf{F} = [F_i\ F_m\ F_r\ F_l]^T$, where T signifies a matrix transpose. To eliminate the effect of enslaving, individual finger forces were transformed into F−modes or force modes, $\mathbf{M} = \mathbf{E}^{-1} \cdot \mathbf{F}$, where $\mathbf{E}$ is a 4 by 4 enslaving matrix (Latash et al., 2002). Every element of E, $E_{i,j}$, is the coefficient of a linear approximation:

$$\boldsymbol{F_{i,j} = f_i^0 + E_{i,j} \cdot F_{TOT,j}},$$

where $F_{i,j}$ is the force produced by finger i, and $F_{TOT,j}$ is the total force of four in the ramp task whose task finger is finger j. Then the Jacobian matrix of this transformation between F_{TOT} and $\mathbf{M}$ is $\mathbf{J} = [1\ 1\ 1\ 1] \cdot \mathbf{E}$.

- Multi−digit correlation indices

The framework of the uncontrolled manifold (UCM) approach (Scholz and Schöner 1999, Scholz, Kang et al. 2003) was used to analyze correlations stabilizing F_{TOT} among F−modes over the cycles detected in the selected phase (10−40 s after t0). Since the sampling numbers in one cycle were different in three frequency conditions, F−modes in each cycle was resampled into 100 samples for the F_{DW} and F_{UP} phases in three frequency conditions. The UCM represents the combinations of individual finger forces do not alter F_{TOT} whose directions can be computed by taking the null space of the Jacobian matrix, J (i.e. orthogonal set of eigenvectors, e_i). For each of the 100 samples within one cycle, the individual mean−free finger forces over those cycles was projected onto these directions (UCM space), summed, and normalized by the MVC and the number of degree of freedom (DOF) to estimate the amount of variance per DOF in the UCM space:

$$\boldsymbol{V_{UCM} = \frac{\sum_{j=1}^{N_{cycles}} \left| \sum_{i=1}^{n-p} (e_i \cdot F) e_i \right|^2}{(n-p) N_{cycles} MVC}},$$

where n = 4 is the number of DOF of individual finger forces, and p

= 1 is the number of DOF of the performance variable (F_{TOT}). Analogously, the amount of variance per DOF orthogonal to the UCM (ORT space) was estimated:

$$V_{ORT} = \frac{\sum_{j=1}^{N_{cycles}} \left| F_{IF} - \sum_{i=1}^{n-p} (e_i \cdot F) e_i \right|^2}{p \ N_{cycles} MVC}.$$

Then ⊿V was calculated as the difference between V_{UCM} and V_{ORT} normalized by the total variance at each of the 100 samples. The average of two variance components (V_{UCM} and V_{ORT}), and ⊿V across samples were estimated as V_{AVG} ($V_{UCM,\ AVG}$ and $V_{ORT,\ AVG}$) and ⊿V_{AVG} for the F_{DW} and F_{UP} phases for each frequency condition and participant. In addition, to investigate the changes within a cycle, V_{DIFF} ($V_{UCM,\ DIFF}$ and $V_{ORT,\ DIFF}$) and ⊿V_{DIFF} was computed as the difference between maximum and minimum of V_{UCM}, V_{ORT} and ⊿V over the 100 examples, respectively.

- Functional connectivity (FC)

Customized Matlab (Matlab 7.4.0, Mathworks, Inc) programs were written for processing fNIRS imaging data. The raw data, changes in optical density, were filtered using discrete cosine transform with frequency range from 0.01 to 0.5 Hz to eliminate high frequency instrumental and surrounding noises. The channel quality was estimated by computing the coefficient of variation (CV):

$$CV = 100 \times \frac{\sigma[I]}{E[I]} (\%),$$

where E[I] and σ[I] denote the mean and standard deviation of optical intensity, respectively. Channels with either a high CV (CV > 40) or a low optical intensity (I < 10) were rejected in further processing including the extraction of hemodynamic data (Shim, Jang et al. 2018). Concentration changes in oxy-hemoglobin (ΔHbO) were calculated via the modified Beer-Lambert law (Delpy, Cope et al. 1988) and band-pass filtered with a 6th order zero-phase Butterworth filter with cutoffs from 0.01 to 0.09 Hz to eliminate systemic noise such as global drifts, Mayer wave, and respiration rate (Scholkmann, Kleiser et al. 2014, Shin, Kwon et al. 2017).

Then Pearson correlation coefficients (r) between ΔHbO signals in each two channels was calculated and average across three trials for each template condition and participant (Figure 5-2). The average magnitude of r (r) in each channel pair was computed by averaging across participant. The statistical significance of r (p) in each channel pair was computed based on a one-sample t-test after applying a Fisher transformation to change r into a normal distribution. Based on the previous studies, the meaningful functional connectivity (FC) was identified as channel pairs possessing high coefficient ($r \ge 0.7$) and statistical significance ($p \le 0.05$) (Cui, Bray et al. 2010). FC analysis were applied to the ΔHbO signals in the whole selected phase (10-40 s after t0), releasing phase only, or pressing phase only. FC between channels located in same (intra-) or different (inter-) hemispheres were counted separately.

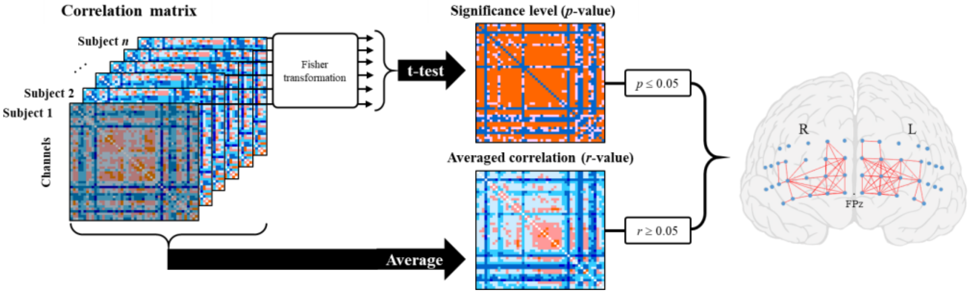

Figure 5-2: Illustration of functional connectivity (FC) analysis.

Illustration of functional connectivity (FC) analysis. Fisher transformation was applied to the averaged correlation matrix for each frequency condition and participant for a t-test. By averaging the correlation matrices of all participants, the meaningful FC between two channels was identified as the high correlation coefficient ($r \ge 0.7$) and the statistical significance ($p \ge 0.05$).

- Statistics

Two-way repeated-measured ANOVAs with the factors of Frequency (three levels: 0.1, 1, and 2 Hz) and Phase (two levels: F_{DW} and F_{UP}) were applied for performance variable as RMSE and correlation indices including ΔV_{AVG} and ΔV_{DIFF}, separately. In addition, two-way repeated-measured ANOVAs with the factors of Frequency (three levels: 0.1, 1, and 2 Hz) and Variance (two levels: V_{UCM} and V_{ORT}) were applied for average and peak-to-peak difference of variance components for the F_{DW} and F_{UP} phases, separately. Mauchly's sphericity test was employed to confirm or reject the assumptions of sphericity. The Greenhouse-Geisser corrections were used when the sphericity assumption was rejected. The statistical power for all comparisons was computed, and for all planned comparisons, the power was over 0.7 from the pool of nine participants. The level of significance for all statistical tests was set at $p < 0.05$.

5.4. Results

5.4.1. Performance

The RMSEs between the total finger force (F_{TOT}) and the concurrent force template in a time-series were calculated for the F_{DW} and F_{UP} phases in the three frequency conditions, separately. Generally, the RMSE showed significant increments with the frequencies for both F_{DW} and F_{UP} phases, and the RMSE was larger in the F_{DW} than in F_{UP} phases, especially at 2 Hz condition. A two-way repeated-measured ANOVA with factors Frequency (three levels: 0.1, 1, and 2 Hz) and Phase (two levels: F_{DW} and F_{UP}) showed significant main effects of Frequency ($F_{[2,\ 8]} = 17.37$, $p < 0.01$) and Phase ($F_{[1,\ 8]} = 20.55$, $p < 0.01$) with a significant Frequency × Phase ($F_{[2,\ 16]} = 6.29$, $p < 0.05$). A significant factor interaction was confirmed by post-hoc comparisons, which showed that the RMSE at 0.1 Hz (0.07) < 1 Hz (0.08) < 2 Hz (0.13) for the F_{UP} phase ($p < 0.05$), while the RMSE at 0.1 Hz (0.07), 1 Hz (0.08) < 2 Hz (0.10) for the F_{DW} phase ($p < 0.05$).

5.4.2 Multi-digit coordination indices

In the F−mode space, two synergy indices including average ΔV (ΔV_{AVG}) and peak−to−peak difference of ΔV (ΔV_{DIFF}) during the F_{UP} and F_{DW} phases were computed based on the time−series of ΔV (Figure 5−3). For both F_{UP} and F_{DW} phases, ΔV_{AVG} were decreased with the frequencies. On average, particularly, ΔV_{AVG} at 2 Hz condition showed negative values for both F_{UP} and F_{DW} phases. On the contrary, ΔV_{DIFF} increased with the frequencies; particularly, ΔV_{DIFF} at 0.1 Hz condition were smaller than ΔV_{DIFF} at other two frequency conditions. These results supported by two−way repeated−measured ANOVAs separately on ΔV_{AVG} and ΔV_{DIFF} with factors Frequency (three levels: 0.1, 1, and 2 Hz) and Phase (two levels: F_{UP} and F_{DW}), which showed a significant main effect of Frequency (ΔV_{AVG}: $F_{[2, 8]} = 29.94$, $p < 0.01$; ΔV_{DIFF}: $F_{[2, 8]} = 14.98$, $p < 0.01$) without factor interactions. Pairwise comparisons confirmed that ΔV_{AVG} at 0.1 Hz > 1 Hz > 2 Hz ($p < 0.05$), while ΔV_{DIFF} at 0.1 Hz < 1 Hz, 2 Hz ($p < 0.05$).

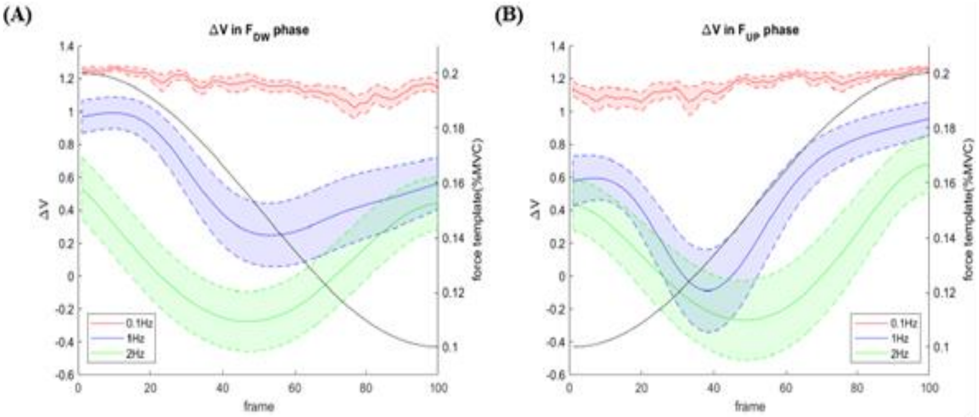

Figure 5−3: The time−series of synergy index and the sample data of force templates.

The time−series of synergy index (ΔV) in three frequency conditions (colorful lines) and the sample data of force templates (black lines) during F_{DW} (A) and F_{UP} (B) phases. The average (solid lines) and standard deviation (dotted lines) across participates were computed at each sample within one cycle.

Further, two components of variance (V_{UCM} and V_{ORT}) were computed in a time-series (Figure 5-4) and applied to investigate the average (V_{AVG}: $V_{UCM, AVG}$ and $V_{ORT, AVG}$) and peak-to-peak difference (V_{DIFF}: $V_{UCM, DIFF}$ and $V_{ORT, DIFF}$) during the F_{UP} and F_{DW} phases. Generally, for both F_{UP} and F_{DW} phases, $V_{ORT, AVG}$ and $V_{ORT, DIFF}$ showed increments with the frequencies while $V_{UCM, AVG}$ and $V_{UCM, DIFF}$ didn't. These results were supported by two-way repeated-measured ANOVAs separately on V_{AVG} and V_{DIFF} for F_{DW} and F_{UP} phases separately with factors Frequency (three levels: 0.1, 1, and 2 Hz) and Variance (two levels: V_{UCM} and V_{ORT}). Effects of Frequency (V_{AVG} for F_{DW}: $F_{[2, 8]} = 25.39$, $p < 0.01$; V_{AVG} for F_{UP}: $F_{[2, 8]} = 62.16$, $p < 0.01$; V_{DIFF} for F_{DW}: $F_{[2, 8]} = 30.25$, $p < 0.01$; V_{DIFF} for F_{UP}: $F_{[2, 8]} = 55.95$, $p < 0.01$) were significant with interactions of Frequency × Variance (V_{AVG} for F_{DW}: $F_{[2, 16]} = 13.46$, $p < 0.01$; V_{AVG} for F_{UP}: $F_{[2, 16]} = 6.4$, $p < 0.05$; V_{DIFF} for F_{DW}: $F_{[2, 8]} = 9.84$, $p < 0.05$; V_{DIFF} for F_{UP}: $F_{[2, 8]} = 5.52$, $p < 0.05$). Pairwise comparisons confirmed the interactions as that only $V_{ORT, AVG}$ and $V_{ORT, DIFF}$ at 0.1 Hz < 1 Hz < 2 Hz ($p < 0.05$) but $V_{UCM, AVG}$ and $V_{UCM, DIFF}$ didn't show significant differences among frequency conditions for both F_{DW} and F_{UP} phases.

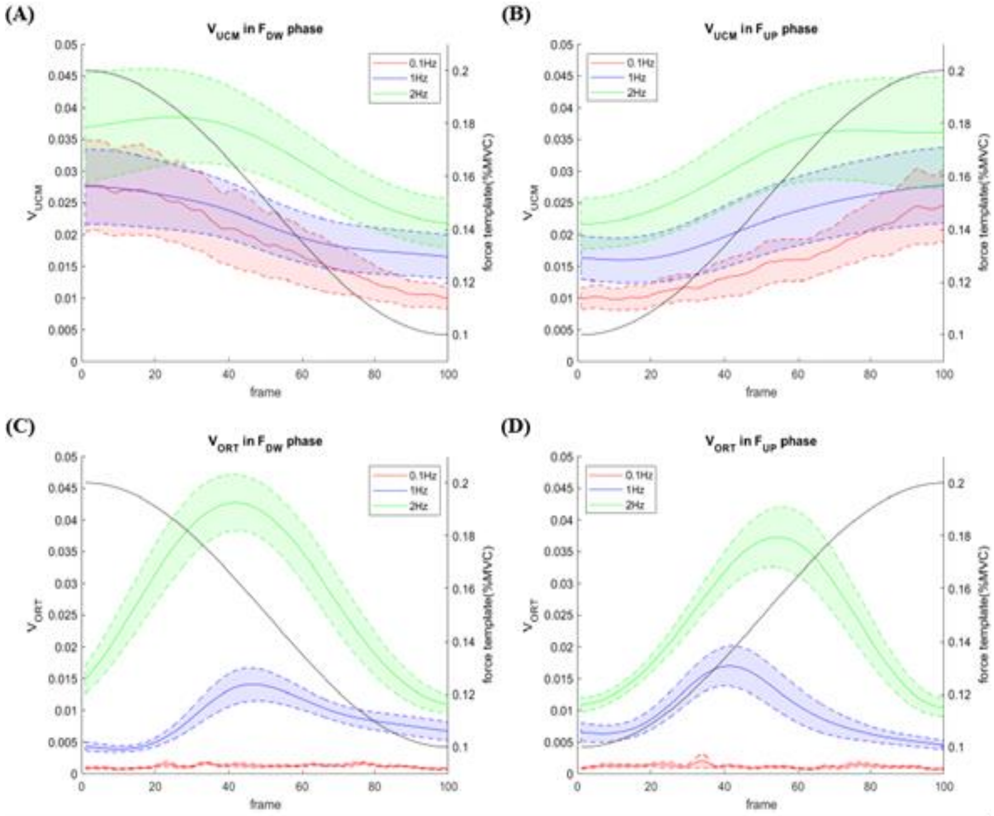

Figure 5−4: The time−series of V_{UCM} and V_{ORT} and the sample data of force templates.

The time−series of V_{UCM} (A and B) and V_{ORT} (C and D) in three frequency conditions (colorful lines) and the sample data of force templates (black lines) during F_{DW} (A and C) and F_{UP} (B and D) phases. The average (solid lines) and standard deviation (dotted lines) across participates were computed at each sample within one cycle.

5.4.3. Functional connectivity (FC)

The FC was investigated as the pair between each two of the total 48 channels which showed high and significant correlation. For FC in the whole selected phase, there were 106 pairs identified as FC in slow condition, which was larger than 50 pairs in middle condition and 61 pairs in fast condition (Figure 5−5). Specially, the number of FC intra left hemispheres were 44, 19, and 24 in three conditions respectively. The number of FC intra right hemispheres were smaller than left hemispheres in all frequency conditions as 29, 8, and 11 in three conditions respectively. The number of FC inter-hemispheres was 54 in slow condition which was larger than 23 in middle and 26 in fast conditions.

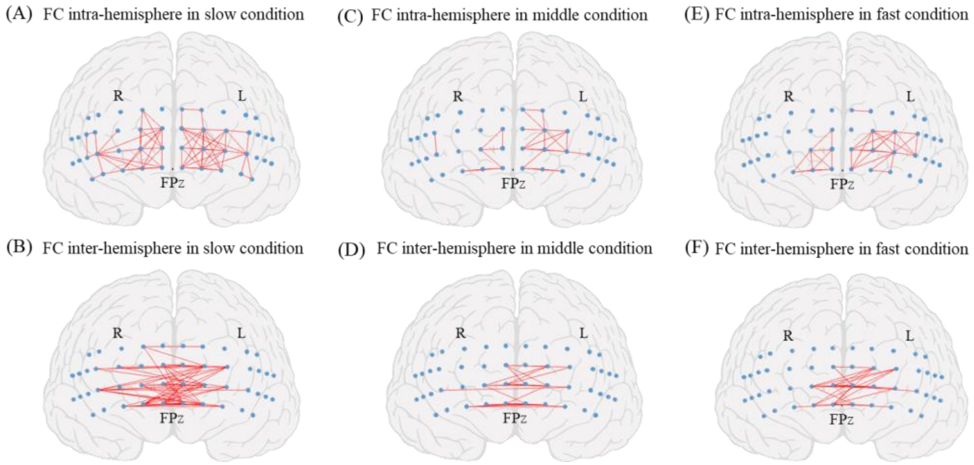

Figure 5-5: FC between channels located in same (intra-) or different (inter-) hemispheres.

FC between channels located in same (intra-) or different (inter-) hemispheres were displayed as red lines. The blue circles describe the location of channels in fNIRS device. A), C), and E) show the FC intra-hemisphere while B), D), and F) show the FC inter-hemisphere in three frequency conditions respectively.

5.5. Discussion

This study investigated the effect of movement frequency on motor control during rhythmic multi-finger force production task. In general, the results showed better performance (i.e., larger accuracy), more stable motor coordination among fingers (i.e., larger synergy index), and higher functional connectivity (FC) in prefrontal cortex (PFC) in low frequency movement.

Rhythmic multi-finger force production task required continuous adaptation of finger forces to product changing target force. The problem was that incorrect contraction of either flexor or extensor serving any individual finger would elicit error in performance while the co-contraction of flexor and extensor influence the coordination among fingers. Specially, the motor signal from central neural system (CNS) was shared among flexors and extensors serving individual fingers during voluntary isometric contraction of finger muscles (Eccles 1968). Therefore, one inherent feature of motor control was to generate stable coordination among elements (cf. individual finger forces) and then, through that, the performance (cf. total force). This stability has recently been estimated through synergy indices (Latash, Scholz et al. 2007, Zhang, Zatsiorsky et al. 2007). The current study showed large and stable synergy index in low frequency movement. Consistently, higher stability in low frequency movement has been reported in multi-joint and multi-limb actions (Abe and Yamada 2003, Kao and Ferris 2005). All these findings implied large and efficient effort towards movement stability in low frequency movement.

The results suggested that the function of PFC in motor control may depend on movement frequency. Prefrontal FC was suggested as a sign of creativity and can be improved by creative training (Wei, Yang et al. 2014). Besides, some neural disorders related to cognitive development could reduce the prefrontal FC (Thiruvady, Georgiou-Karistianis et al. 2007, Ye, Peng et al. 2012). Therefore, the decrease of prefrontal FC implied temporarily suppressed cognitive process in high movement frequency. The suppressed cognition may linkage to the obstruction in motor control since cognition plays an important role in motor control especially in motor planning (Vahdat, Darainy et al. 2011, Gentsch, Weber et al. 2016) and motor adaptation (Taylor and Thoroughman 2008, King, Bruetsch et al. 2013). Besides, the changes in cognitive process could be detected as the prefrontal FC which supports the PFC as a region involved in motor planning (Berchicci, Lucci et al. 2012). Several studies investigated the discrepancy in motor control caused by frequency to distinguish discrete and rhythmic movements (Sternad and Dean 2003, Schaal, Sternad et al. 2004, Hogan and Sternad 2007). For instance, several higher cortical planning areas was activated in discrete movement while motor-related areas in rhythmic movements (Hogan and Sternad 2007). The higher prefrontal FC in low frequency movement supported the idea that frequency is a characteristic to distinguish discrete and rhythmic movements and eliciting different motor control process.

In another sight, feedback and feedforward processes have emerged as two important components in motor control to interpret experimental phenomenon including brain activation (Kuo 2002, Seidler, Noll et al. 2004). Among which, feedforward control is considered as a predictive process based on prior knowledge and without regard to the consequences of the action (Kawato 1999, Friston 2011) as a cognitive process. The function of PFC was supposed to be related to feedforward process in motor control. For instance, many studies reported the increment of PFC oxygenation when the goal of following movement need to be adapted (Sadato, Ibañez et al. 1997, Agnew, Zeffiro et al. 2004, Kuboyama, Nabetani et al. 2005, Ishii, Liang et al. 2018). However, the PFC oxygenation maintained during continuous movements even with different properties including the results in the current study (Jenkins, Passingham et al. 1997, Kim, Eliassen et al. 2005). These findings imply the role of PFC in goal-directed motor adaptation as a feedforward process. In addition, higher FC in PFC was observed in slower movement. This effect of frequency was consistent with the effect of difficulty in mental tasks such as decision making and behavioral selection (Clausen, Francisco et al. 2017, Maes, Swinnen et al. 2020, Mussini, Berchicci et al. 2020). It suggested that increased frequency didn’t elicit goal-directed motor adaption but make the existing feedforward process more difficulty. Oppositely, feedback control represents the process of regulating the motor command from the CNS based on sensation includes visual, auditory, somatic, and other sensory information (Jordan and Wolpert 1999). Previous studies have demonstrated less effect of the absent of feedback information on performance during fast movement comparing to slow movement (Hay and Bard 1984, Beaubaton and

Hay 1986, Messier, Adamovich et al. 2003). Therefore, the contribution of feedback process in motor control may be reduced by increased movement frequency. Besides, visual feedback information can help generate stable coordination in low frequency movement (Yamagata, Popow et al. 2019, Huang, Van Syoc et al. 2020). In summary, the contribution of feedback process and the efficiency of feedforward and cognitive processes may reduce with increased movement frequency, which led to less stability and worse performance.

5.6 Conclusion

This study demonstrated the motor stability and cognitive neural activity in response to movement frequency which indicated the contribution of cognitive and feedforward processes in the formation of speed–accuracy tradeoff and the linkage between cognitive process and motor stability. These findings may indicate selection of movement speed rather than accuracy by adapting the efficiency of cognitive process.

Chapter 6. Effect of Sensory Modality: Multi-Sensory Integration during Multi-Digit Rotation Task with Different Frequency

6.1. Abstract

Speed−accuracy tradeoff (SAT) revealed the negative relation between response speed and response accuracy during motor tasks with an influence of sensory processing. Multi−sensory integration, as an efficient way to improve motor performance, was supposed as a factor of the SAT. Eight subjects were required to rotate a handle following one of three frequencies provided by visual or auditory sensory feedback or synchronically both. Rotated angle were measured to compute the difference between measured and required angles as performance. Multi−sensory integration was estimated by comparing the measured performance to the computed value based on maximum likelihood estimation (MLE). As results, multi−sensory integration succeed only in fast frequency condition. However, the coordination among fingers didn’t change with the successful integration. These results suggest that the efficiency of multi−sensory integration depends on movement speed and beyond the generation of motor synergy.

6.2. Introduction

Speed−accuracy tradeoff (SAT) revealed the negative relation between response speed and response accuracy during mental tasks such as decision making and motor tasks such as multi−joint reaching, multi−digit rotation (Plamondon and Alimi 1997). It is widely investigated that the phenomenon of SAT holds the influence of sensory modality, for instance, by comparing the reaction time under visual, audio, and haptic feedback (Alais and Burr 2004, Li, Wang et al. 2018). In traditional sight, the mechanism of SAT was considered as the limit of information evidence such as response thresholds and sensory gain (Ditterich 2006, Donkin, Little et al. 2014, Standage, Blohm et al. 2014). Recently, the neural mechanism of the SAT has received an increasing attention and the influence of sensory processing on the SAT has been proposed by two opposite opinions. Some studies suggested the manipulation in the late stage of motor control such as the activity of pre-motor areas (see reviews in Heitz 2014) while a few studies reported the changes in the early stage such as sensory process in primary visual cortex (V1) (Rinkenauer, Osman et al. 2004, Heitz and Schall 2012, Ho, Brown et al. 2012). In addition, the decrement of sensory cortex activation was demonstrated in fast movement in previous chapters. Therefore, further investigation was proposed to the effects of sensory process in motor control strategy and motor performance, especially the speed and accuracy.

Multi-sensory integration is widely used paradigm in the investigation of sensory process. Lots of studies reported improved motor performance including shorter reactive time, larger accuracy, and more effective learning when provided additional sensory information (Spidalieri, Busby et al. 1983, Burke, Prewett et al. 2006, Laurienti, Burdette et al. 2006, Sigrist, Rauter et al. 2013). This phenomenon has been described as the integration of different sensory modalities which interprets the merger of multiple, and often redundant, sources of information about the changing body state and environment (Andersen, Tiippana et al. 2005, Liu, Sinclair et al. 2008, Ronsse, Miall et al. 2009, Meijer, Veselič et al. 2019). Models have been established to describe multi-sensory integration by assuming optimality such as Bayesian model or maximum likelihood estimation (MLE) that is different signal sources are weighted by the inverse of their variance, greater weight being given to the more reliable source (Ronsse, Miall et al. 2009, Brayanov and Smith 2010). However, the neural mechanism of multi-sensory integration is still unclear since its influence occurs in wide areas in human brain (see reviews in Murray and Wallace 2011) including sensory areas (Heitz and Schall 2012), motor cortex (Spidalieri, Busby et al. 1983), and prefrontal cortex (Clark, Christou et al. 2014). At least, changed sensory process can be convinced in responsible for the improved motor performance.

Therefore, multi-sensory integration was supposed to be a factor of the SAT since it is an efficient way to improve sensory process and, in consequence, motor performance. Accordingly, the purpose of this study was to compare the efficiency of the multi-sensory integration during multi-digit rotation actions with different movement speed. The hypothesis was that the reduced accuracy when required high movement speed may be improved by additional sensory information.

6.3. Method

6.3.1. Subjects

Eight right-hand dominant young males (age 30.3 ± 2.7 years, height 167.49 ± 6.53 m, mass: 69.39 ± 15.73 kg) volunteered for to the current experiment. All the participants had no medical records of neurological disorders and upper extremity injury including forearm, hand, and fingers. Seoul National University Institutional Review Board (IRB) approved the use of customized experimental protocol related to multi-finger rotation tasks and compatible devices including a customized experimental frame, force transducers, and encoder. All the experimental details were performed in accordance with the relevant guidelines and regulations. The consent was informed, and all the participants were requested to sign a consent form approved by the IRB at Seoul National University (IRB No. 2007/002-028).

6.3.2. Apparatus

Five six-component force transducers (Nano-17, ATI Industrial Automation, Garner, NC, USA) were used to measure forces of three axes produced by five fingers of right hand. The sensors (size ϕ17mm × 14.5mm) were attached to a customized flat aluminum plane (size 150 mm × 19 mm × 3mm). One sensor was at the center of one side while other four sensors were symmetrically located at the other side which composed the rotated handle (Figure 6-1B). Added weights, which had same shape and weight with the sensors, were attached to the counter side of the handle for each sensor to balance the weight of two sides and made the initial center of the handle at the center of the plane. Each sensor was covered with sandpaper (300-grit) to increase the friction between the finger-tips and the top surface of the sensors. The center of the rotation handle was fixed on the table while the handle was allowed rotating along the axis passing through the center in a 2D-space. The force signals measured by force sensors were digitized at 200 HZ using a customized Labview (National Instruments, Austin, TX, USA) program. Synchronically, an encoder (AHS36A, SICK STEGMANN GmbH, DE, Germany) was attached to the center of the handle to measure its rotated angle sampling as 200 Hz.

A computer screen in front of subjects provided visual feedback of the required rotation frequency with a resolution as 1068 × 1050. A red bar was projected in the center of the screen and cyclically rotated around the center from −45° to 45° with respect to the vertical orientation as 0° (Figure 6.1C). A pair of earphones was used to provide auditory feedback. Simple tone sound cyclically turned up and then down alternately in the left and right channels. The tone of the sound was 500 Hz while the range of the changed volume of the sound was from 25 dB to 50 dB (Figure 6-1D).

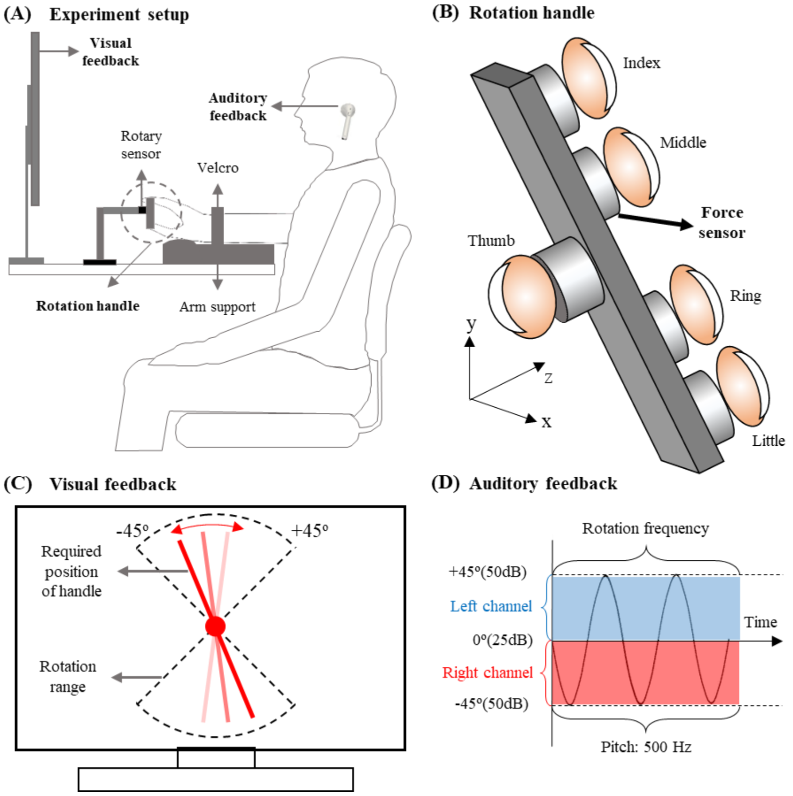

Figure 6–1: Illustration of the experimental setup in sensory–based multi–digit rotation task.

Illustration of the experimental setup. A) The subjects lied on the PET scanner, wore a paired of deluxe prism glasses, and hold a customized rotated handle. B) The feedback screen displayed the real–time posture of the handle and a slipper metronome. C) Three force sensors were attached to a vertically oriented aluminum plane.

6.3.3. Procedures

Subjects sat in front of the computer screen and wore earphones while holding the customized handle with five fingers of right hand above the five force transducers (Figure 6.1A). Their right upper arm was put on a wrist–forearm brace and fixed to the table. The main task was cyclically rotating the handle from –45° (pronation) to 45° (supination) with respect to the vertical orientation as 0° following the frequency provided by visual or auditory feedback or synchronically both. There were three conditions of sensory modality as 1) visual, 2) auditory, and 3) visual + auditory, and three conditions of frequency as 1) slow (0.1 Hz), 2) middle (0.5 Hz), 3) fast (1 Hz). In total, each subject performed tasks in combined nine conditions and three trials in each condition with a randomized sequence. Because the official experiment, subjects practiced the rotation action for 15–20 min until the accuracy of performance was above 50% computed based on the difference between measured and required angles (see more in Data Processing). Each trial continued 20 cycles which means continuing 200s in slow condition, 40s in middle condition, and 20s in fast condition. 5min rest was provided after each trial.

6.3.4. Data analysis

- Performance

Customized Matlab (Matlab 7.4.0, Mathworks, Inc) programs were written for angle and force data analyses. The measured angle signal was digitally low–pass filtered with a 2th–order Butterworth filter at 10 Hz cut–off. The angle data during the first and last of the 20 cycles were excluded from the following analysis. Then the average and standard–deviation (SD) of root–mean squared error (RMSE) across repetitive trials were computed as performance; that was the differences between measured and required angles.

Through the average and SD of RMSE in visual and auditory conditions, the theoretical distribution of RMSE under multi–sensory integration was computed based on the method of maximum likelihood estimation (MLE) (Koh, Kwon et al. 2016):

$$\mu_{MLE} = \omega_V \mu_V + \omega_A \mu_A \ , \omega_V = \frac{\sigma_V^2}{\sigma_V^2+\sigma_A^2} \ , \omega_A = \frac{\sigma_A^2}{\sigma_V^2+\sigma_A^2};$$

where μ and σ refer to the average and SD of RMSE; subscript V, A and MLE refer to visual, auditory conditions and computed value based on MLE. Then the computed average of RMSE was compared to the measured performance in visual + auditory condition.

- Finger force data

The force signals were digitally low–pass filtered with a 2th–

order Butterworth filter at 10 Hz cut-off. The force and moment data during the first and last of the 20 cycles were excluded from the following analysis. Virtual finger (VF) forces and moments were calculated as the vector sum of individual finger (IF, i.e. index, middle, ring, and little fingers) forces and moments. A hierarchical control of the CNS based on the concept of VF has been suggested as a possible strategy to generate a desired task performance (Gorniak, Zatsiorsky et al. 2007, Latash, Gorniak et al. 2008). Note that the action of the VF can be the same as mechanical effects produced by IF. The analysis was performed both at the VF level. According to the experimental requirement, the following constraint of moment existed during the task:

$$M_n^{vf}(t) + M_t^{th}(t) + M_t^{vf}(t) = I\alpha(t),$$
$$M_n^{vf}(t) = F_n^{vf}(t) \cdot D^{vf};$$

where subscript n and t refer to the normal and tangential force components; superscripts th and vf refer to thumb and VF; M represents the moment of forces respect to the center of the handle (which means the moment of F_n^{th} was zero); D represents the moment arm of normal forces; I and α represent the moment of inertia and angular acceleration in the rotation plane, respectively. Note that moments of thumb or VF were the sum of moments of normal and tangential force components. Specially, the moment arm of tangential forces was a constant as the width of the handle. Each cycle was separated into pronation phase (i.e., rotation angle from 45° to −45°) and supination phase (i.e., rotation angle from −45° to 45°). For both pronation and supination phases, the moments of thumb and VF were computed in a time sequence in every cycle.

- Multi-digit correlation indices

The framework of the uncontrolled manifold (UCM) approach (Scholz and Schöner 1999, Latash, Scholz et al. 2002) was used to analyze correlations stabilizing moments over the cycles detected in the both pronation and supination phases. Since the sampling numbers in one cycle were different in three frequency conditions, moments of thumb and VF in both phases in each cycle was resampled into 100 samples in three frequency conditions. The UCM represents the combinations of moments do not alter total moment whose directions can be computed by taking the null space of the Jacobian matrix, J (i.e. orthogonal set of eigenvectors, ei). For each of the 100 samples within one cycle, the mean-free moments over those cycles were projected onto these directions (UCM space), summed while the number of degree of freedom (DOF) to estimate the amount of variance per DOF in the UCM space:

$$V_{UCM} = \frac{\sum_{j=1}^{N_{cycles}} \left| \sum_{i=1}^{n-p} (e_i \cdot F) e_i \right|^2}{(n-p) N_{cycles}},$$

where n = 2 is the number of DOF of moment in VF level, and p = 1 is the number of DOF of the performance variable (M_{TOT}). Analogously, the amount of variance per DOF orthogonal to the UCM (ORT space) was estimated:

$$V_{ORT} = \frac{\sum_{j=1}^{N_{cycles}} \left| F_{IF} - \sum_{i=1}^{n-p} (e_i \cdot F) e_i \right|^2}{p \ N_{cycles} MVC}.$$

Then ΔV was calculated as the difference between V_{UCM} and V_{ORT} normalized by the total variance at each of the 100 samples. ΔV across samples were estimated for the pronation and supination phases for each frequency condition and participant.

- Statistics

Two-way repeated-measured ANOVAs with the factors of Frequency (three levels: slow, middle, and fast) and Sensory modality (three levels: visual, auditory, and visual + auditory) were applied for performance variable as RMSE and correlation indices as ΔV separately. In addition, two-way repeated-measured ANOVAs with the factors of Frequency (three levels: slow, middle, and fast) and Sensory modality (two levels: visual + auditory and MLE) were applied for comparing the measured performance in visual + auditory condition and the computed RMSE based on MLE. Mauchly's sphericity test was employed to confirm or reject the assumptions of sphericity. The Greenhouse-Geisser corrections were used when the sphericity assumption was rejected. The statistical power for all comparisons was computed, and for all planned comparisons, the power was over 0.7 from the pool of eight participants. The level of significance for all statistical tests was set at $p < 0.05$.

6.4. Results

6.4.1 Performance

Generally, RMSE between measured and required rotation angle were increased with speed in both visual and auditory conditions. However, in visual + auditory condition, the RMSE showed a decrease in fast speed condition. As a result, the measured RMSE in visual + auditory conditions was larger than RMSE computed by MLE in slow and middle conditions but similar with the computed RMSE in visual + auditory condition (Figure 6-2). A two-way repeated measured ANOVA with factors of Speed (three levels: slow, middle, and fast) and Sensory modality (three levels: visual, auditory, and visual + auditory) showed significant main effect of Speed ($F_{[2, 8]} = 20.23$, $p < 0.01$) with a significant Speed × Sensory modality ($F_{[2, 16]} = 22.93$, $p < 0.01$). In addition, Another two-way repeated measured ANOVA with factors of Speed (three levels: slow, middle, and fast) and Sensory modality (two levels: visual + auditory and MLE) showed significant main effect of Speed ($F_{[2, 8]} = 8.70$, $p < 0.05$) without significant interaction of Speed × Sensory modality.

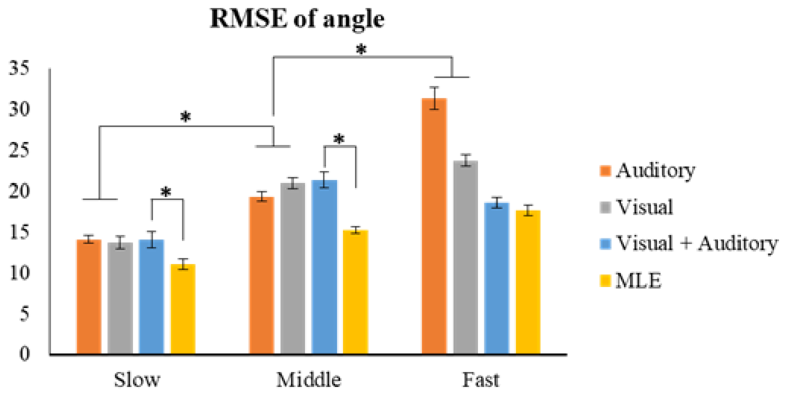

Figure 6-2: RMSE measured in 9 conditions and computed based on maximum likelihood estimation.

6.4.2 Multi-digit coordination indices

Synergy index decreased with speed in all three sensory modality conditions supported by a two-way repeated measured ANOVA on ΔV with factors of Speed (three levels: slow, middle, and fast) and Sensory modality (three levels: visual, auditory, and visual + auditory) showed significant main effect of Speed ($F_{[2, 8]} = 15.15$, $p < 0.01$) without significant interaction of Speed × Sensory modality during both pronation and supination phases (Figure 6-3).

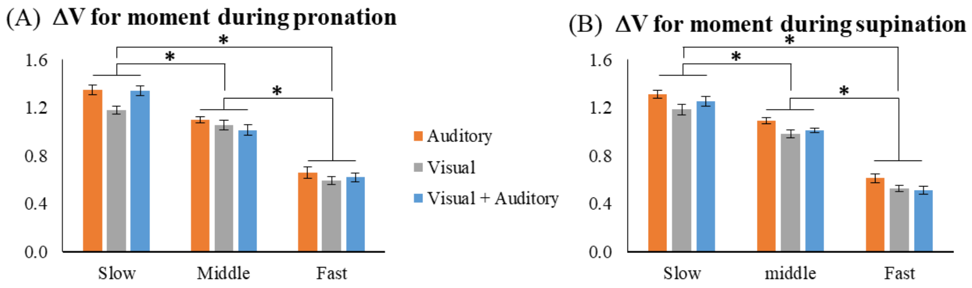

Figure 6.3: Synergy index in 9 experimental conditions during pronation and supination phases.

Synergy index averaged across participants in 9 experimental conditions during pronation (A) and supination (B) phases.

6.5. Discussion

In this study, performance and coordination among fingers were investigated during multi-digit rhythmic rotation task with different frequencies. Generally, increased speed incited worse performance and smaller synergy index. Specially, the results showed improved performance when receiving both visual and auditory information in fast speed condition rather than slow and middle speed conditions. However, there was no change in synergy index associate with the success of multi-sensory integration in fast speed condition.

The changes of performance in response to movement frequency were consistent with results in previous chapters which can be well explained by speed-accuracy tradeoff. Similarly, the decreased motor variability (coordination among fingers) caused by increased movement frequency was consistent with previous studies (Almeida, Wishart et al. 2002, Huang, Van Syoc et al. 2020). It provided more evidences interpreting the mechanism of speed-accuracy tradeoff in terms of stability or variability. That is the reduced variability could be considered as a sign of restriction in the motor control system which elicited worse performance.

Successful multi-sensory integration in fast speed condition supported the hypothesis as multi-sensory integration will improve the accuracy in high speed movement. It indicated multiple sensory information were combined in fast condition in the manner of maximum likelihood estimation. Due to this, sensory process may become more efficiency to provide accurate resource in motor control. It supported the hypothesis that the rate of sensory evidence accumulation necessarily limits the efficacy of downstream decision making and motor control processes (Beyeler, Dutt et al. 2013). In the basis, speed-accuracy tradeoff should relate to the inaccuracy or less accumulated sensory information in fast condition.

Although performance conspicuous improved through multi-sensory integration, the motor variability maintained in a low level during fast movement. It implied the generation of motor variability separated with the sensory process, especially the process of combining multiple sensory information. Same studies suggested the generation of variability in the spinal cord level (Shah, Gerasimenko et al. 2012, Macefield 2013). However, others studies showed the relation between variance components and activity in brain regions (Van Horn, Grafton et al. 2008, Palva and Palva 2011, Rana, Yani et al. 2015, Babikian, Kanso et al. 2017). Specially, the variance doesn't affect the performance (V_{UCM}) more likely relate to motor control under intention (Klous, Mikulic et al. 2011, Latash and Huang 2015, Park and Xu 2017) while the variance does affect the performance (V_{ORT}) more likely relate to automatic motor adaptation (Ferber, Osternig et al. 2002, Brooks, Garcia et al. 2016). This study didn't measure the neural activation and was short of evidence to discuss the generation of motor variability. At least, it should be separated with the process of sensory integration. In the future, it is expected to see studies measure neural activation during multi-sensory integration during fast movement.

6.6 Conclusion

This study observed the success of multi-sensory integration during fast movement. It suggested that the efficiency of multi-sensory integration depends on movement speed and beyond the generation of motor synergy. The effect of movement speed on the quality of sensory process and its possible consequence as speed-accuracy tradeoff have been discussed.

Chapter 7. Effect of Task Complexity: Prefrontal Cortex Oxygenation during Multi-Digit Pressing Actions with Different Frequency Components

7.1. Abstract

Task difficulty or complexity associates with the mental effort and cognitive process. In addition, speed−accuracy tradeoff was discussed as a consequence of reduced cognitive efficiency during fast movement. To investigate the effect of task complexity on cognitive process, eight subjects were required to cyclically pressing and releasing using four fingers following the given template with three levels of complexity. The prefrontal cortex oxygenation was measured and translated into the function connectivity. The difference between measured total finger force and concurrent template target force were computed to describe performance. As results, motor variability and prefrontal functional connectivity decreased with task complexity associate with a worse performance. These findings provided evidence for the effect of difficulty on the efficiency of cognitive process. In addition, the effect of task complexity on cognitive process and motor variability were homogeneous but stronger than frequency.

7.2. Introduction

Task complexity was mentioned as a factor in task taxonomy since 1970s (Farina, Wheaton et al. 1971, Fleishman 1975). Traditionally, task complexity was defined and investigated in two separate sights as task characteristic (Earley 1985) and cognitive process during goal setting (Locke, Frederick et al. 1984). With the increase of objective complexity as a task characteristic, it caused multiple possible types of outcomes satisfying task requirements, multiple possible pathways to achieve a certain outcome, and even uncertain relation between outcomes and pathways (see reviews in Campbell 1988). Along of the widely application in multiple paradigms, the discrimination of task complexity has developed into, for instance, the number of decision sequences (Holper, Biallas et al. 2009, Holper and Wolf 2011), degree of contextual interference (Jarus and Gutman 2001, Verstynen, Diedrichsen et al. 2005), or number of task components (Laguna 2008, Mussini, Berchicci et al. 2020). The current study supposed to classify the level of task complexity by the number of frequency components in the required action. Since the effect of single frequency on cognitive process has been investigated in chapter 5, the following idea was the effect of task complexity and its interaction with frequency.

Numerous studies have investigated the effect of task complexity and demonstrated reduced performance in both mental and motor tasks, for instance, decrease in action or selection accuracy (Ishibuchi and Nojima 2005, Robinson and Gilabert 2007) and increase in reaction time (Bentin and McCarthy 1994, Edquist, Rudin-Brown et al. 2012). Further, the long-term effects of task complexity were also verified through the decreased efficiency in motor learning and skill acquirement (Robinson and Gilabert 2007, Laguna 2008). Specially, task complexity deteriorated the coordination among elements in motor tasks containing large-scale movement like sit-up task (Cordo and Gurfinkel 2004) and small-scale movement like prehension (Krishnan and Jaric 2010). For details, increased task complexity was associate with unstable coordination patterns between upper and lower limbs during walk/clap task (Getchell and Whitall 2003). In addition, the decrease in stable coordination or increase in mobility were observed with increased task complexity when considering the coordination between left and right limbs (Krishnan and Jaric 2010), or among muscles defined as muscle synergy (Cordo and Gurfinkel 2004, Frère and Hug 2012). Traditionally, motor coordination was considered as a consequence of the problem of motor redundancy (Bernstein 1967). Recently, the principle of abundance was proposed through studies about multi-digit human actions (Latash

2000) and suggested that motor control system prefers to utilize motor coordination to generate flexible and stable performance. Therefore, the negative effect of task complexity on performance and motor coordination suggested some effects in motor control. However, these effects were usually described by observing the motor outcomes while the neural mechanism was still unclear.

Benefit to the development of approaches in neurophysiology such as functional near-infrared spectroscopy (fNIRS), neural activity of the brain became measureable during motor tasks which promoted the investigation of neural mechanism in motor control. Studies reported a consistent phenomenon that neural activity were differed in relation to task complexity during multiple types of motor tasks. For instance, activity of primary motor cortex (M1) increased with task complexity (Verstynen, Diedrichsen et al. 2005, Holper, Biallas et al. 2009, Holper and Wolf 2011). Specially, several recent studies reported reduced functional connectivity (FC) in prefrontal cortex (PFC) during complex tasks (Lew, Rey et al. 2008, Maes, Swinnen et al. 2020, Mussini, Berchicci et al. 2020). The FC in PFC has been widely investigated in neuroscience and suggested the influence of cognitive process (Rissman, Gazzaley et al. 2004, Wei, Yang et al. 2014, Clausen, Francisco et al. 2017, Krukow, Jonak et al. 2018). Besides, recall that the definition of task complexity which implied a relation to cognitive process. This motivated the hypothesis that task complexity may affects the cognitive process associate with the FC in PFC, which contributes to the motor control and leads to reduced motor coordination and performance. Therefore, the purpose of this study was to verify the effect of task complexity on motor coordination and cognitive process during multi-digit force production tasks. It will reveal the contribution of cognitive process to motor control, especially the control of coordinated motor behaviors, and help understanding the neural mechanism of motor control.

7.3. Method

7.3.1. Subjects

Eight right−hand dominant young males (age 30.3 ± 2.7 years, height 167.49 ± 6.53 m, mass: 69.39 ± 15.73 kg) volunteered for to the current experiment. All the participants had no medical records of neurological disorders and upper extremity injury including forearm, hand, and fingers. Seoul National University Institutional Review Board (IRB) approved the use of customized experimental protocol related to multi−finger pressing tasks and compatible devices including a customized experimental frame, force transducers, and fNIRS device. All the experimental details were performed in accordance with the relevant guidelines and regulations. The consent was informed, and all the participants were requested to sign a consent form approved by the IRB at Seoul National University (IRB No. 2007/002−028).

7.3.2. Apparatus

Depth−dependent hemodynamic changes in the PFC were recorded using a wearable NIRST fNIRS device (NIRSIT, OBELAB, Seoul, Korea) at a sampling rate of 9 Hz. While no ambient light blocking was performed except for firm contact on a forehead, we confirmed that ambient light did not affect the NIRS data by confirming that channel quality is kept at an appropriate level before and during the experiments. NIRSIT captures depth−dependent hemodynamic changes in the PFC, because a number of NIRS channels can be configured with a variety of source−detector (SD) separations. However, in the current study, we used only typical lattice−arranged SD separations which was 30mm.

Four force sensors (Nano−17, ATI Industrial Automation, Garner, NC) were used to measure pressing forces (i.e., normal forces) being attached to a customized flat panel (140 × 90 mm) as shown in Figure 7−1B. Only normal forces (along Z−axis) were measured. Each sensor was covered with a cotton pad in order to increase the friction. On the panel, there were four slots along the

X−axis, which were used to attach the sensors, and the sensor positions were adjusted along the slots according to the individual hand and finger size of each subject. The distance between the slots was 3.0 cm in the medio−lateral direction (Figure 7−1B). The panel was mechanically fixed to the immovable table. A total of four analogue signals from the sensors related to the normal force components were digitized with a 16−bit analogue–digital converters (USB−6225, National Instrument, Austin, TX) with the help of a customized LabVIEW program (LabVIEW 8.0, National Instrument, Austin, TX). Before each trial, all signals from the sensors were zeroed. The sampling frequency was set at 200 Hz.

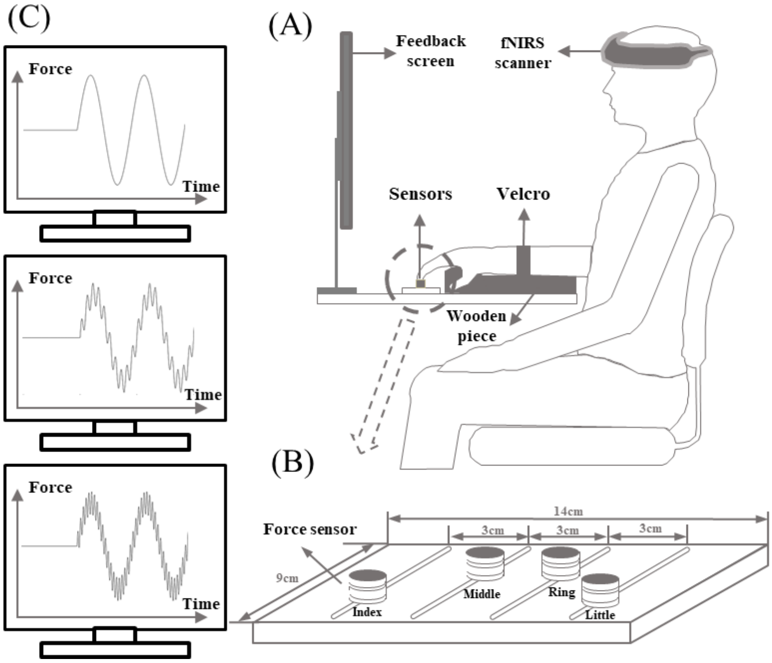

Figure 7−1: Illustration of the experimental setup in complexity−based multi−digit pressing task.

Illustration of the experimental setup (A). The subject’ s wrist was held stationary with Velcro straps. A wooden cylinder supported the palm, and the force sensors were attached to a frame (B). The feedback screen displayed the real−time finger forces and showed the templates combined by different sine waves during force production tasks (C).

7.3.3. Procedures

Subjects sat in a height−adjustable chair facing the computer screen and positioned their right upper arm on a wrist−forearm brace that was fixed to the table. Each subject had an orientation session to become familiar with the experimental devices and to ensure that the subject was able to perform the experimental tasks. The forearm was held stationary with Velcro straps to prevent forearm and wrist movement, and the fingertips were placed on the centers of sensors (Figure 7−1A). A wooden piece was placed underneath the subject’s right palm in order to ensure a constant configuration of hand and fingers during finger force production.

At the beginning, the maximal voluntary contraction (MVC) force using four fingers was measured for each participant and utilized in the setup of the main task. In the main task, the participants were asked to produce cyclic sine−wave−like total finger forces (Figure 7−1C). The force templates consisted of the combinations of sine waves that had different frequencies with same amplitude (10% of MVC force of four fingers). There were three complexity conditions for the force templates including 1) 0.1 HZ, 2) 0.1+1HZ (combination of 0.1HZ sine wave and 1HZ sine wave), and 3) 0.1+1+2HZ (combination of 0.1HZ, 1HZ, and 2HZ sine waves). Each trial consists of three blocks which has a 40 s steady state force production followed by 50 s cyclic pressing with random one of the three templates and 30 s rest. The 40 s steady state was designed to elicit a stable hemodynamic state before cyclic force production which utilized as a baseline in analyzing fNIRS imaging data (Cui, Bray et al. 2010). The 50 s cyclic state was designed to elicit several cycles for applying UCM analysis (i.e. see more details in ‘Data analysis) without the effect of fatigue. Every participant had a 10−20 min practice until the performance index (i.e. see more details in ‘Data analysis) was less than 0.2 to ensure that the participant was able to perform the experimental tasks. After the orientation session and enough rest, each participant performed three trials with a 5 min rest between each two trials. Each trial consisted of three blocks in which the three frequency conditions were displayed in a random sequence with a 30 s rest between each two blocks.

7.3.4. Data analysis

- Performance

Customized Matlab (Matlab 7.4.0, Mathworks, Inc) programs were written for force and fNIRS data analyses. For the force data analysis, individual finger forces (i.e. index finger force: F_i; middle finger force: F_m; ring finger force: F_r; little finger force: F_l) were digitally low-pass filtered with a 4th-order Butterworth filter at 10 Hz cut-off.

The time at the start of cyclic force production was defined as t_0. Each cycle of the template during 10-40 s after t_0 was detected. The root mean square (RMSE) of F_{TOT} error (i.e. difference between measured F_{TOT} and the concurrent template force) was computed and normalized by the center level of target force (i.e., 15% of MVC). The average of RMSE across three trials was estimated as the performance for each condition and participant.

- Multi-finger correlation indices

The framework of the uncontrolled manifold (UCM) approach (Scholz and Schöner 1999, Scholz, Kang et al. 2003) was used to analyze correlations stabilizing FTOT over the samples detected in selected phase (10-40 s after t_0). Since the sampling numbers in one cycle were different in three frequency conditions, moments of thumb and VF in both phases in each cycle was resampled into 100 samples in three complexity conditions. The UCM represents the combinations of individual finger forces do not alter FTOT whose directions can be computed by taking the null space of the Jacobian matrix, J (i.e. orthogonal set of eigenvectors, e_i). For each of the 100 samples within one cycle, the mean-free finger forces over those samples were projected onto these directions (UCM space), summed while the number of degree of freedom (DOF) to estimate the amount of variance per DOF in the UCM space:

$$V_{UCM} = \frac{\sum_{j=1}^{N_{cycles}} \left| \sum_{i=1}^{n-p} (e_i \cdot F) e_i \right|^2}{(n-p) N_{cycles}} ,$$

where n = 4 is the number of DOF of individual finger forces, and p = 1 is the number of DOF of the performance variable (F_{TOT}). Analogously, the amount of variance per DOF orthogonal to the UCM (ORT space) was estimated:

$$V_{ORT} = \frac{\sum_{j=1}^{N_{cycles}} \left| F_{IF} - \sum_{i=1}^{n-p} (e_i \cdot F) e_i \right|^2}{p \;\; N_{cycles} MVC} .$$

Then ΔV was calculated as the difference between V_{UCM} and V_{ORT} normalized by the total variance at each of the 100 samples. The average of two variance components (V_{UCM} and V_{ORT}), and ΔV across samples were estimated for each frequency condition and participant.

- Functional connectivity (FC)

Customized Matlab (Matlab 7.4.0, Mathworks, Inc) programs were written for fNIRS imaging data processing. The raw data for light intensity were filtered using discrete cosine transform with frequency range from 0.01 to 0.5 Hz to eliminate high frequency instrumental and surrounding noises. The channel quality was determined from the coefficient of variation (CV), defined based on the following criteria:

$$CV = 100 \times \frac{\sigma[I]}{E[I]} (\%) ,$$

where E[I] and σ[I] denote the mean and standard deviation of optical intensity, respectively. Channels with either a high CV (CV > 40) or a low optical intensity (I < 10) were rejected in further processing including the extraction of hemodynamic data (Shin el al., 2018). Concentration changes in oxy-hemoglobin (ΔHbO) were calculated via the modified Beer-Lambert law (Delpy, Cope et al. 1988) and band-pass filtered with a 6th order zero-phase Butterworth filter with cutoffs from 0.01 to 0.09 Hz to eliminate systemic noise such as global drifts, Mayer wave, and respiration rate (Scholkmann, Kleiser et al. 2014, Shin, Kwon et al. 2017).

Then Pearson correlation coefficients (r) between ΔHbO signals in each two channels was calculated and average across three trials for each template condition and participant (Figure 5-2). The average magnitude of r (r) in each channel pair was computed by averaging across participant. The statistical significance of r (p) in each channel pair was computed based on a one-sample t-test after applying a Fisher transformation to change r into a normal distribution. Based on the previous studies, the meaningful functional connectivity (FC) was identified as channel pairs possessing high coefficient ($r \geq 0.7$) and statistical significance ($p \leq 0.05$) (Cui el al., 2010). FC analysis were applied to the ΔHbO signals in the whole selected phase (10-40 s after t0), releasing phase only, or pressing phase only. FC between channels located in same (intra-) or different (inter-) hemispheres were counted separately.

- Statistics

One-way repeated-measured ANOVAs with the factors of Complexity (three levels: 0.1, 0.1+1, and 0.1+1+2 HZ) were applied for performance variable as RMSE and correlation indices including V_{UCM}, V_{ORT}, and ΔV, separately. In addition, two-way repeated-measured ANOVAs with the factors of Complexity (three levels: 0.1, 1, and 2 HZ) and Variance (two levels: V_{UCM} and V_{ORT}) were applied for average of variance components. Mauchly's sphericity test was employed to confirm or reject the assumptions of sphericity. The Greenhouse-Geisser corrections were used when the sphericity assumption was rejected. The statistical power for all comparisons was computed, and for all planned comparisons, the power was over 0.7 from the pool of nine participants. The level of significance for all statistical tests was set at $p < 0.05$.

7.4. Results

7.4.1. Performance

The RMSE between the total finger force (F_{TOT}) and the concurrent force template in a time-series were calculated in the three complexity conditions, separately. Generally, the RMSE showed significant increments with the complexity (Figure 7−2). A one−way repeated−measured ANOVA with factor of Complexity (three levels: 0.1, 0.1+1, and 0.1+1+2 HZ) showed significant effect of Complexity ($F_{[2,\ 8]}$ = 232.14, $p < 0.01$). The averaged and normalized RMSE were 0.036 ± 0.004 in 0.1HZ condition, 0.118 ± 0.009 in 0.1+1HZ condition, and 0.219 ± 0.014 in 0.1+1+2HZ.

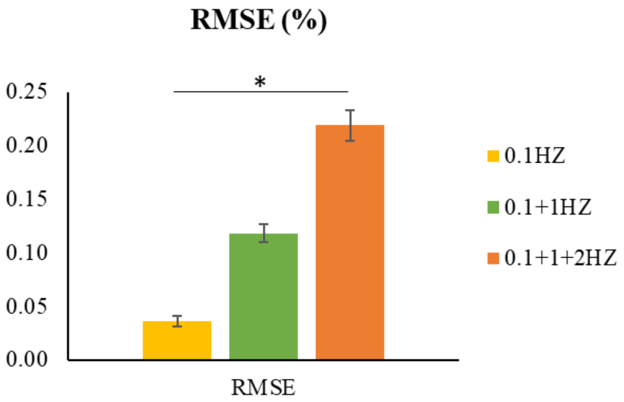

Figure 7−2: RMSE averaged across trials and normalized by 15% of MVC in three complexity conditions.

7.4.2. Multi-finger coordination indices

Synergy indices including averaged variance components (V_{UCM} and V_{ORT}) and ΔV across participates. Two variance components increased with complexity while ΔV decreased with complexity (Figure 7−3). A two−way repeated−measured ANOVA on variance components with factors of Complexity (three levels: 0.1, 0.1+1, and 0.1+1+2 HZ) and Variance (two levels: V_{UCM} and V_{ORT}) showed significant effects of Complexity ($F_{[2,\ 8]}$ = 41.91, $p < 0.01$) and Variance ($F_{[1,\ 8]}$ = 16.14, $p < 0.01$) with a significant interaction of Complexity × Variance ($F_{[2,\ 16]}$ = 35.34, $p < 0.01$). The significant factor interaction was confirmed by post−hoc comparisons, which showed that the V_{UCM} was larger than V_{ORT} in 0.1HZ condition but smaller than V_{ORT} in 0.1+1HZ and 0.1+1+2HZ conditions. In addition, ΔV was positive in 0.1HZ condition while negative in

0.1+1HZ and 0.1+1+2HZ conditions. A one−way repeated−measured ANOVA on ΔV with factor of Complexity (three levels: 0.1, 0.1+1, and 0.1+1+2 HZ) showed significant effect of Complexity ($F_{[2, 8]} = 135.30$, $p < 0.01$).

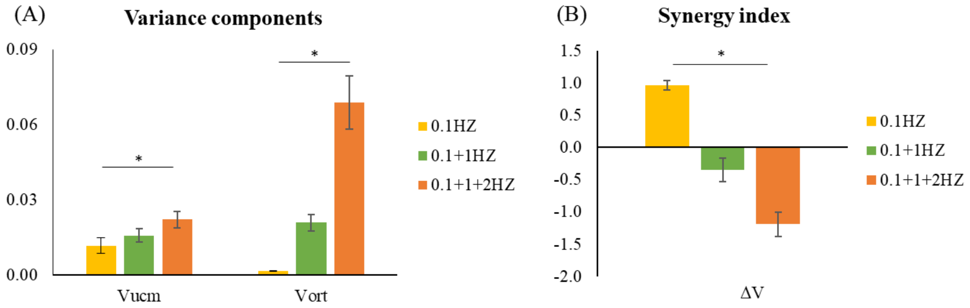

Figure 7−3: V_{UCM}, V_{ORT} (A) and ΔV (B) averaged across participates in three complexity conditions.

7.4.3. Functional connectivity (FC)

The FC was investigated as the pairs between each two of the total 48 channels which showed high and significant correlation. For FC in the whole selected phase, there were 110 pairs identified as FC in 1Hz condition, which was larger than 43 pairs in 0.1+1Hz condition and 39 pairs in 0.1+1+2Hz condition (Figure 7−4). Specially, the number of FC intra right hemispheres were 38, 24, and 20 in three complexity conditions respectively. The number of FC intra left hemispheres were smaller than right hemispheres in all frequency conditions as 30, 8, and 7 in three conditions respectively. The number of FC inter−hemispheres was 42 in 0.1Hz condition which was larger than 11 in 0.1+1Hz and 12 in 0.1+1+2Hz conditions.

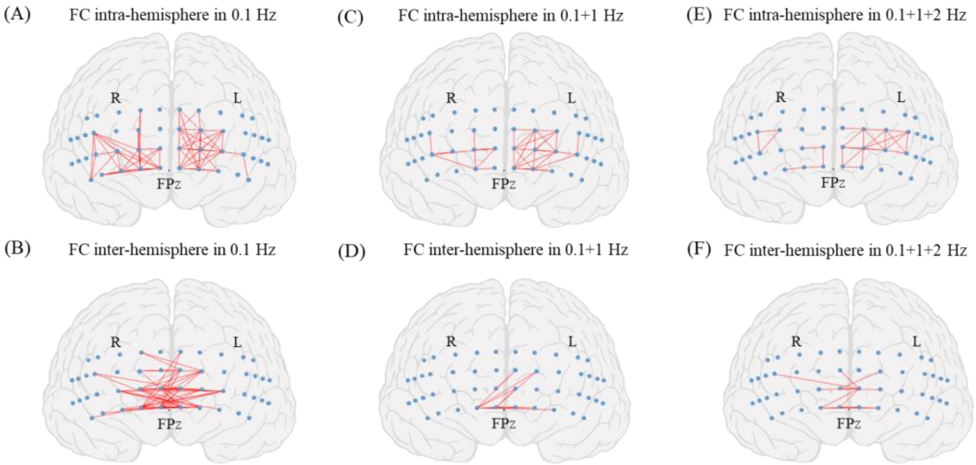

Figure 7−4: FC between channels located in same (intra−) or different (inter−) hemispheres

FC between channels located in same (intra−) or different (inter−) hemispheres were displayed as red lines. The blue circles describe the location of channels in fNIRS device. A), C), and E) show the FC intra−hemisphere while B), D), and F) show the FC inter−hemisphere in three complexity conditions respectively.

7.5. Discussion

7.5.1. Relation between Frequency and task complexity

To be noticed, this study designed a new type of task complexity based on the combination of frequency components in motor requirement. In a viewpoint of structural constitution, the concept of task complexity was continuously and widely described in two dimensions in lots of mental tasks [see reviews in (Liu and Li 2012)]. One is the number of possible stimulus types to be provided (Madarsara and Rahimy 2015, Mussini, Berchicci et al. 2020) or possible decisions to be selected (Meister, Krings et al. 2005) such as the fingers during finger tapping (Holper, Biallas et al. 2009, Holper and Wolf 2011). Another one is the degree of the difference between adjacent decisions or behaviors to be excepted (Laguna 2008, Mussini, Berchicci et al. 2020) such as the concept of contextual interference (Jarus and Gutman 2001). It implied that the task complexity depends on the combination of several single behaviors. Interestingly, rhythmic movement with one frequency component was considered as a single action in motor tasks. Numerous of studies investigated the separation between rhythmic and discrete movements using experimental paradigms and theoretical constructs [see reviews in (Degallier and Ijspeert 2010)]. Furthermore, these two types of movements were considered to be interlinked and constitute primitives for complex actions in daily life (Sternad, Dean et al. 2000, Jirsa and Scott Kelso 2005, Hogan and Sternad 2007). Therefore, although it is an uncommon motor goal, the combination of several rhythmic movements with different frequencies could be a more complex action than rhythmic movement with a single frequency.

Generally, longer reaction time (RT) were observed in more complex tasks no matter for young or elderly or people with neural disorders when subjects were required to perform as fast as they can [see reviews in (Campbell 1988)]. However, without the pressure of speed requirement, the longer reaction time in more complex conditions might not be replicated (Van Donkelaar and Franks 1991, Ma and Trombly 2004). Therefore, the effect of motor complexity may affect by movement speed. When considering rhythmic movements, the frequency of movement is also possible to be a factor of motor complexity as discussed in chapter 5. Hence, the combination of movement frequencies contains both the effect of frequency and the changes in element components. Since the experiment procedure and data analysis in this study was consistent with those in chapter 5, the results in two studies were comparable.

7.5.2 Cognitive process in motor control

The investigation of task complexity has emphasized involvement of cognitive process, such as cognitive demands (Campbell 1988, Wickens and McCarley 2007) and cognitive effort (Bettman, Johnson et al. 1990). The cognitive process in complex task associated with decision making requires divergent process and creativity (DeLuca and Stumpf 1981), even correlates with intelligence quotient (Larson, Merritt et al. 1988). Relevantly, prefrontal FC was suggested as a sign of creativity and can be improved by creative training (Wei, Yang et al. 2014). Besides, smaller prefrontal FC was found in subjects with neurological disorders related to cognitive functions, such as attention‐deficit/hyperactivity disorder (Wolf, Plichta et al. 2009), psychopathy (Contreras−Rodríguez, Pujol et al. 2015), schizophrenia (Chai, Whitfield−Gabrieli et al. 2011), etc. Logically, the difference in prefrontal FC could be temporarily suppressed by adjustment of neural activation or durative impaired due to abnormal brain structure. Obviously, the reduced prefrontal FC caused by task complexity is temporary since it will restore immediately when subjects transferred to simple tasks. Therefore, the reduced prefrontal FC suggests suppressed cognitive process, in other words, reduced efficiency of cognitive process. This seems to be opposite with the traditional understanding of complex task which suggested the requirement of more cognitive effort in complex task (Chu and Spires 2000, Speier 2006).

To be noticed, the requirement of more cognitive effort was the inference based on the basic characteristic of cognitive process in mental tasks such as decision making (Wang and Ruhe 2007). However, if the cognitive effort increased as required, what is the reason made the performance still worse? More primarily, whether the cognitive effort increased as required? In modern view, behavior control is the integration of cognitive process in relation to task goal−setting and habitual control based on stimulus−response mapping (Redgrave, Rodriguez et al. 2010, Cushman and Morris 2015). It well explained the phenomenon that after enough practice, even the most complex tasks will become habitual (Scott Jr and Erskine 1980). Hence, the evaluation of task complexity should consider the stage of control including the innovation stage and the stabilization stage (Kozlowski and Hults 1986). After enough practice, behaviors become habitual and more stable (Wu, Pazin et al. 2013, Wu and Latash 2014) with reduced cognitive load (Haith and Krakauer 2018). Although without the measurement of cognitive process during learning, this study tried to reject the learning effect by applying enough practice until the relatively stable and accuracy performance were performed and by random sequence of task complexity conditions. Even though, the efficiency of cognitive process reduced with task complexity which rejected the requirement of more cognitive effort. Therefore, we suggested that the suppressed cognitive process was not the requirement of complex task but the strategy of control the CNS selected. With the high requirement of cognitive effort caused by task complexity, the CNS chose to reduce the efficiency of cognitive process and perform more habitual actions. However, the limitation of this study is the absence of the sensory process related measurement which could be utilized to verify the habitual control differed by task complexity.

7.5.3 Relation between motor coordination and cognitive process

Recall the hypothesis established in last paragraph that the CNS chose to reduce the efficiency of cognitive process in tasks with high frequency-based complexity. Simultaneously, the motor coordination among fingers was reduced based on uncontrolled manifold (UCM) computation. The motor coordination in this study represents the ability to perform stable performance with sharing among fingers (Bernstein 1967). Previous studies have demonstrated the problems in motor coordination among children with neurodevelopmental disorders such as autism spectrum disorder (Higashionna, Iwanaga et al. 2017), attention deficit/hyperactivity disorder (Watemberg, Waiserberg et al. 2007) and specific learning disorder (Westendorp, Hartman et al. 2011). The decreased cognitive abilities in those children were associate with the problems to establish motor coordination (Watemberg, Waiserberg et al. 2007, Westendorp, Hartman et al. 2011, Higashionna, Iwanaga et al. 2017). Furthermore, the negative effect of task complexity on motor coordination were consistent with the reduced cognitive efficiency. It implied the motor coordination as a sign of cognitive efficiency. Theories such as internal model were proposed to describe the cognitive process in motor control as motor planning or programming based on experimental observation and simulation results (Kawato 1999, Grafton 2010). However, the neural mechanism of motor coordination including cognitive process is still unclear. The results of this study pointed the importance of prefrontal FC in the generation of motor coordination. Further investigations are excepted to reveal the neural activation during motor control.

7.6 Conclusion

This study demonstrated the motor coordination and cognitive neural activity in response to task complexity and indicated its effect on the efficiency of cognitive process which led to worse stability and accuracy as performance. Specially, the effect of complexity was stronger than the effect of movement frequency. In addition, these finding provided evidence for in the mechanism of speed–accuracy tradeoff and the linkage between cognitive process and motor coordination.

Chapter 8. Conclusions and Future Work

8.1. Summary of conclusions

1. When multi–digit force production action changes its direction, an anticipatory adjustment exists no matter the direction is. However, no difference between the directional conditions suggests that feedforward synergy adjustment (changes in the stability property) may be at least independent of the magnitude of the task–specific apparent performance variables and its direction (e.g., flexion and extension forces).

2. During rhythmic multi–digit rotation actions, two sets of brain regions function differently which showed involvements of cognitive and sensory processes respectively. The function of sensory process was reduced with the increase of movement frequency. Furthermore, the effect of task difficulty based on movement frequency was discussed on the relative contributions of cognitive and sensory processes.

3. During rhythmic multi–digit pressing actions, correlation among digits and prefrontal FC decreased with movement speed, associate with worse performance (accuracy). These findings provide evident for the linkage between cognitive process and the generation of coordination during multi–digit human actions. Besides, the mechanism of speed–accuracy tradeoff (SAT) was suggested to be the selection of movement speed with relative changes in the efficiency of cognitive process.

4. During rhythmic multi–digit rotation actions, multi–sensory integration succeeds only in fast frequency condition. However, the coordination among digits didn’t change with the successful integration. These results suggested that the efficiency of multi–sensory integration depends on movement speed and beyond the generation of motor synergy.

5. During rhythmic multi–digit pressing actions, motor variability and prefrontal FC decreased with task complexity

associate with a worse performance. These findings provided more evidences for the effect of difficulty on the efficiency of cognitive process. In addition, the effect of task complexity on cognitive process and motor variability were homogeneous but stronger than frequency.

8.2. Future work

In summary, this thesis tried to investigate the role of sensory and cognitive processes in motor control, especially the control of motor variability in redundant human motor system. Through several experiments, it has been demonstrated that both the sensory and cognitive processes involved in almost every action of humans. Specially, the contributions of sensory and cognitive processes were quantified under several conditions. However, a development or impairment in sensory or cognitive process would elicit great changes in motor outcomes differently. Therefore, in the future, it is expected to investigate the effect of frequency, sensory modality, complexity on aging, fatigue, and neural disorders.

Besides, motor variability has considered as an important character of motor outcomes related to multiple levels in motor control such as performance and brain activity. Therefore, it is hopeful to detect the dysfunction in sensory and cognitive processes in the early stage based on the measurement of multi-digit actions. It will be more wearable and popular since the measurement is much more comfortable then current measurement method.

At last, the properties affect then sensory and cognitive processes would be useful to develop training method or assistant devices for better motor outcomes. It can be a benefit for the increasing elder population and neural patients.

Bibliography

Abe, M. O. and N. Yamada (2003). "Modulation of elbow joint stiffness in a vertical plane during cyclic movement at lower or higher frequencies than natural frequency." Experimental brain research 153(3): 394–399.

Agnew, J. A., T. A. Zeffiro and G. F. Eden (2004). "Left hemisphere specialization for the control of voluntary movement rate." Neuroimage 22(1): 289–303.

Alais, D. and D. Burr (2004). "The ventriloquist effect results from near–optimal bimodal integration." Current biology 14(3): 257–262.

Alexander, G. E., M. D. Crutcher and M. R. DeLong (1991). Basal ganglia–thalamocortical circuits: parallel substrates for motor, oculomotor,“prefrontal” and “limbic” functions. Progress in brain research, Elsevier. 85: 119–146.

Almeida, Q. J., L. R. Wishart and T. D. Lee (2002). "Bimanual coordination deficits with Parkinson's disease: the influence of movement speed and external cueing." Movement Disorders 17(1): 30–37.

Ambike, S., V. M. Zatsiorsky and M. L. Latash (2015). "Processes underlying unintentional finger–force changes in the absence of visual feedback." Experimental brain research 233(3): 711–721.

Andersen, T. S., K. Tiippana and M. Sams (2005). "Maximum likelihood integration of rapid flashes and beeps." Neuroscience letters 380(1–2): 155–160.

Arpinar–Avsar, P., J. Park, V. M. Zatsiorsky and M. L. Latash (2013). "Effects of muscle vibration on multi–finger interaction and coordination." Experimental brain research 229(1): 103–111.

Aruin, A. S. and M. L. Latash (1995). "Directional specificity of postural muscles in feed–forward postural reactions during fast voluntary arm movements." Experimental brain research 103(2): 323–332.

Aupperle, R. L., A. J. Melrose, A. Francisco, M. P. Paulus and M. B. Stein (2015). "Neural substrates of approach - avoidance conflict decision - making." Human brain mapping 36(2): 449–462.

Babikian, S., E. Kanso and J. J. Kutch (2017). "Cortical activity predicts good variation in human motor output." Experimental brain research 235(4): 1139–1147.

Bajaj, S., D. Drake, A. J. Butler and M. Dhamala (2014). "Oscillatory motor network activity during rest and movement: an fNIRS study." Frontiers in Systems Neuroscience 8: 13.

Balleine, B. W. and A. Dickinson (1998). "Goal–directed instrumental action: contingency and incentive learning and their cortical substrates." Neuropharmacology 37(4–5): 407–419.

Bandura, A. and R. Wood (1989). "Effect of perceived controllability and performance standards on self–regulation of complex decision making." Journal of personality and social psychology 56(5): 805.

Barbas, H. and D. Pandya (1989). "Architecture and intrinsic connections of the prefrontal cortex in the rhesus monkey." Journal of Comparative Neurology 286(3): 353–375.

Barraclough, D. J., M. L. Conroy and D. Lee (2004). "Prefrontal cortex and decision making in a mixed–strategy game." Nature neuroscience 7(4): 404–410.

Barrett, K. E., S. M. Barman, S. Boitano and H. Brooks (2009). "Ganong's review of medical physiology. 23." NY: McGraw–Hill Medical.

Baud–Bovy, G. and J. F. Soechting (2001). "Two virtual fingers in the control of the tripod grasp." Journal of Neurophysiology 86(2): 604–615.

Beaubaton, D. and L. Hay (1986). "Contribution of visual information to feedforward and feedback processes in rapid pointing movements." Human Movement Science 5(1): 19–34.

Bentin, S. and G. McCarthy (1994). "The effects of immediate stimulus repetition on reaction time and event–related potentials in tasks of different complexity." Journal of Experimental Psychology: Learning, Memory, and Cognition 20(1): 130.

Berchicci, M., G. Lucci, C. Pesce, D. Spinelli and F. Di Russo (2012). "Prefrontal hyperactivity in older people during motor planning." Neuroimage 62(3): 1750-1760.

Bernstein, N. A. (1967). "The co-ordination and regulation of movements."

Bertelli, J. (2015). "Tendon palpation during agonist contraction and antagonist co-contraction to assess wrist flexor and extensor muscle function." Chirurgie de la main 34(2): 79-85.

Bettman, J. R., E. J. Johnson and J. W. Payne (1990). "A componential analysis of cognitive effort in choice." Organizational behavior and human decision processes 45(1): 111-139.

Beyeler, M., N. D. Dutt and J. L. Krichmar (2013). "Categorization and decision-making in a neurobiologically plausible spiking network using a STDP-like learning rule." Neural Networks 48: 109-124.

Bizzi, E., A. d'Avella, P. Saltiel and M. Tresch (2002). "Book review: Modular organization of spinal motor systems." The Neuroscientist 8(5): 437-442.

Black, D. P., B. A. Smith, J. Wu and B. D. Ulrich (2007). "Uncontrolled manifold analysis of segmental angle variability during walking: preadolescents with and without Down syndrome." Experimental brain research 183(4): 511-521.

Bleuse, S., F. Cassim, J. L. Blatt, E. Labyt, J. L. Bourriez, P. Derambure, A. Destée and L. Defebvre (2008). "Anticipatory postural adjustments associated with arm movement in Parkinson's disease: a biomechanical analysis." Journal of Neurology, Neurosurgery & Psychiatry 79(8): 881-887.

Blundell, C., B. Uria, A. Pritzel, Y. Li, A. Ruderman, J. Z. Leibo, J. Rae, D. Wierstra and D. Hassabis (2016). "Model-free episodic control." arXiv preprint arXiv:1606.04460.

Bogacz, R., E.-J. Wagenmakers, B. U. Forstmann and S. Nieuwenhuis (2010). "The neural basis of the speed–accuracy tradeoff." Trends in neurosciences 33(1): 10-16.

Bosch, T., S. E. Mathiassen, B. Visser, M. d. Looze and J. v. Dieën

(2011). "The effect of work pace on workload, motor variability and fatigue during simulated light assembly work." Ergonomics 54(2): 154-168.

Bove, M., A. Tacchino, A. Novellino, C. Trompetto, G. Abbruzzese and M. F. Ghilardi (2007). "The effects of rate and sequence complexity on repetitive finger movements." Brain research 1153: 84-91.

Brayanov, J. B. and M. A. Smith (2010). "Bayesian and "anti-Bayesian" biases in sensory integration for action and perception in the size–weight illusion." Journal of neurophysiology 103(3): 1518-1531.

Brodmann, K. (2007). Brodmann's: Localisation in the cerebral cortex, Springer Science & Business Media.

Brooks, J. R., J. O. Garcia, S. E. Kerick and J. M. Vettel (2016). "Differential functionality of right and left parietal activity in controlling a motor vehicle." Frontiers in systems neuroscience 10: 106.

Brooks, J. X. and K. E. Cullen (2019). "Predictive sensing: The role of motor signals in sensory processing." Biological Psychiatry: Cognitive Neuroscience and Neuroimaging 4(9): 842-850.

Burke, J. L., M. S. Prewett, A. A. Gray, L. Yang, F. R. Stilson, M. D. Coovert, L. R. Elliot and E. Redden (2006). Comparing the effects of visual-auditory and visual-tactile feedback on user performance: a meta-analysis. Proceedings of the 8th international conference on Multimodal interfaces.

Caçola, P., M. Ibana, M. Ricard and C. Gabbard (2016). "Children with developmental coordination disorder demonstrate a spatial mismatch when estimating coincident-timing ability with tools." Research in developmental disabilities 48: 124-131.

Campbell, D. J. (1988). "Task complexity: A review and analysis." Academy of management review 13(1): 40-52.

Cavanagh, P. R. and P. V. Komi (1979). "Electromechanical delay in human skeletal muscle under concentric and eccentric contractions." European journal of applied physiology and occupational physiology 42(3): 159-163.

Chai, X. J., S. Whitfield-Gabrieli, A. K. Shinn, J. D. Gabrieli, A. N. Castanón, J. M. McCarthy, B. M. Cohen and D. Öngür (2011). "Abnormal medial prefrontal cortex resting-state connectivity in bipolar disorder and schizophrenia." Neuropsychopharmacology 36(10): 2009-2017.

Chen, X., Y. Yuan, S. Cao, X. Zhang and X. Chen (2018). "A SEMG-force estimation framework based on a fast orthogonal search method coupled with factorization algorithms." Sensors 18(7): 2238.

Cho, Z.-H., H.-K. Min, S.-H. Oh, J.-Y. Han, C.-W. Park, J.-G. Chi, Y.-B. Kim, S. H. Paek, A. M. Lozano and K. H. Lee (2010). "Direct visualization of deep brain stimulation targets in Parkinson disease with the use of 7-tesla magnetic resonance imaging." Journal of neurosurgery 113(3): 639-647.

Chu, P.-C. and E. E. Spires (2000). "The joint effects of effort and quality on decision strategy choice with computerized decision aids." Decision Sciences 31(2): 259-292.

Churchland, M. M., M. Y. Byron, S. I. Ryu, G. Santhanam and K. V. Shenoy (2006). "Neural variability in premotor cortex provides a signature of motor preparation." Journal of Neuroscience 26(14): 3697-3712.

Churchland, M. M., J. P. Cunningham, M. T. Kaufman, J. D. Foster, P. Nuyujukian, S. I. Ryu and K. V. Shenoy (2012). "Neural population dynamics during reaching." Nature 487(7405): 51-56.

Chye, L., K. Nosaka, L. Murray, D. Edwards and G. Thickbroom (2010). "Corticomotor excitability of wrist flexor and extensor muscles during active and passive movement." Human movement science 29(4): 494-501.

Clark, D. J., E. A. Christou, S. A. Ring, J. B. Williamson and L. Doty (2014). "Enhanced somatosensory feedback reduces prefrontal cortical activity during walking in older adults." Journals of Gerontology Series A: Biomedical Sciences and Medical Sciences 69(11): 1422-1428.

Clausen, A. N., A. J. Francisco, J. Thelen, J. Bruce, L. E. Martin, J. McDowd, W. K. Simmons and R. L. Aupperle (2017). "PTSD and cognitive symptoms relate to inhibition‐related prefrontal activation and functional connectivity." Depression and anxiety 34(5): 427–436.

Claxton, L. J., R. Keen and M. E. McCarty (2003). "Evidence of motor planning in infant reaching behavior." Psychological Science 14(4): 354–356.

Cluff, T., F. Crevecoeur and S. H. Scott (2015). "A perspective on multisensory integration and rapid perturbation responses." Vision research 110: 215–222.

Cockburn, A., P. Quinn, C. Gutwin, G. Ramos and J. Looser (2011). "Air pointing: Design and evaluation of spatial target acquisition with and without visual feedback." International Journal of Human–Computer Studies 69(6): 401–414.

Colebatch, J., M. Deiber, R. Passingham, K. Friston and R. Frackowiak (1991). "Regional cerebral blood flow during voluntary arm and hand movements in human subjects." Journal of neurophysiology 65(6): 1392–1401.

Connor, S. (2004). The book of skin, Cornell University Press.

Contreras–Rodríguez, O., J. Pujol, I. Batalla, B. J. Harrison, C. Soriano–Mas, J. Deus, M. López–Solà, D. Macià, V. Pera and R. Hernández–Ribas (2015). "Functional connectivity bias in the prefrontal cortex of psychopaths." Biological Psychiatry 78(9): 647–655.

Corcos, D. M., G. L. Gottlieb, M. L. Latash, G. L. Almeida and G. C. Agarwal (1992). "Electromechanical delay: An experimental artifact." Journal of Electromyography and Kinesiology 2(2): 59–68.

Cordo, P. J. and V. S. Gurfinkel (2004). Motor coordination can be fully understood only by studying complex movements. Progress in brain research, Elsevier. 143: 29–38.

Cramer, S. C., E. L. Orr, M. J. Cohen and M. G. Lacourse (2007). "Effects of motor imagery training after chronic, complete spinal cord injury." Experimental brain research 177(2): 233–242.

Crammond, D. J. and J. F. Kalaska (1996). "Differential relation of discharge in primary motor cortex and premotor cortex to movements versus actively maintained postures during a reaching task." Experimental brain research 108(1): 45-61.

Cui, H. and R. A. Andersen (2007). "Posterior parietal cortex encodes autonomously selected motor plans." Neuron 56(3): 552-559.

Cui, X., S. Bray and A. L. Reiss (2010). "Functional near infrared spectroscopy (NIRS) signal improvement based on negative correlation between oxygenated and deoxygenated hemoglobin dynamics." Neuroimage 49(4): 3039-3046.

Cushman, F. and A. Morris (2015). "Habitual control of goal selection in humans." Proceedings of the National Academy of Sciences 112(45): 13817-13822.

Danion, F., M. Latash, Z.-M. Li and V. Zatsiorsky (2001). "The effect of a fatiguing exercise by the index finger on single-and multi-finger force production tasks." Experimental brain research 138(3): 322-329.

Danion, F., M. Latash, Z. Li and V. Zatsiorsky (2000). "The effect of fatigue on multifinger co-ordination in force production tasks in humans." The Journal of physiology 523(Pt 2): 523.

Danion, F., G. Schöner, M. L. Latash, S. Li, J. P. Scholz and V. M. Zatsiorsky (2003). "A mode hypothesis for finger interaction during multi-finger force-production tasks." Biological cybernetics 88(2): 91-98.

Darainy, M., S. Vahdat and D. J. Ostry (2013). "Perceptual learning in sensorimotor adaptation." Journal of neurophysiology 110(9): 2152-2162.

Davies, J., D. Parker, O. Rutherford and D. Jones (1988). "Changes in strength and cross sectional area of the elbow flexors as a result of isometric strength training." European journal of applied physiology and occupational physiology 57(6): 667-670.

Daw, N. D., Y. Niv and P. Dayan (2005). "Uncertainty-based competition between prefrontal and dorsolateral striatal systems for behavioral control." Nature neuroscience 8(12): 1704-1711.

de Abreu, L. P. F., T. Teodoro and M. J. Edwards (2018). Neuroimaging Applications in Functional Movement Disorders.

International review of neurobiology, Elsevier. 143: 163–177.

de Freitas, S. M. S. F. and J. P. Scholz (2010). "A comparison of methods for identifying the Jacobian for uncontrolled manifold variance analysis." Journal of biomechanics 43(4): 775–777.

De Houwer, J., G. Crombez, F. Baeyens and D. Hermans (2001). "On the generality of the affective Simon effect." Cognition & Emotion 15(2): 189–206.

Degallier, S. and A. Ijspeert (2010). "Modeling discrete and rhythmic movements through motor primitives: a review." Biological cybernetics 103(4): 319–338.

Delis, I., B. Berret, T. Pozzo and S. Panzeri (2013). "Quantitative evaluation of muscle synergy models: a single–trial task decoding approach." Frontiers in computational neuroscience 7: 8.

Delpy, D. T., M. Cope, P. van der Zee, S. Arridge, S. Wray and J. Wyatt (1988). "Estimation of optical pathlength through tissue from direct time of flight measurement." Physics in Medicine & Biology 33(12): 1433.

DeLuca, J. R. and S. A. Stumpf (1981). Problem solving and decision making: A proposed differentiation, New York University, Graduate School of Business Administration.

Dennerlein, J. T., D. B. Martin and C. Hasser (2000). Force–feedback improves performance for steering and combined steering–targeting tasks. Proceedings of the SIGCHI conference on Human Factors in Computing Systems.

Desmurget, M. and S. Grafton (2000). "Forward modeling allows feedback control for fast reaching movements." Trends in cognitive sciences 4(11): 423–431.

DeWolf, T. and C. Eliasmith (2011). "The neural optimal control hierarchy for motor control." Journal of neural engineering 8(6): 065009.

Dickinson, A. and B. Balleine (1994). "Motivational control of goal–directed action." Animal Learning & Behavior 22(1): 1–18.

Diedrichsen, J., R. Shadmehr and R. B. Ivry (2010). "The coordination of movement: optimal feedback control and beyond." Trends in cognitive sciences 14(1): 31–39.

Dieterich, M. and T. Brandt (2018). The parietal lobe and the vestibular system. Handbook of clinical neurology, Elsevier. 151: 119–140.

Dietz, V. (2003). "Spinal cord pattern generators for locomotion." Clinical Neurophysiology 114(8): 1379–1389.

Dingwell, J. B. and L. C. Marin (2006). "Kinematic variability and local dynamic stability of upper body motions when walking at different speeds." Journal of biomechanics 39(3): 444–452.

Disbrow, E., E. Litinas, G. H. Recanzone, J. Padberg and L. Krubitzer (2003). "Cortical connections of the second somatosensory area and the parietal ventral area in macaque monkeys." Journal of Comparative Neurology 462(4): 382–399.

Ditterich, J. (2006). "Evidence for time‐variant decision making." European Journal of Neuroscience 24(12): 3628–3641.

Donkin, C., D. R. Little and J. W. Houpt (2014). "Assessing the speed–accuracy trade–off effect on the capacity of information processing." Journal of Experimental Psychology: Human Perception and Performance 40(3): 1183.

Dum, R. P., D. J. Levinthal and P. L. Strick (2016). "Motor, cognitive, and affective areas of the cerebral cortex influence the adrenal medulla." Proceedings of the National Academy of Sciences 113(35): 9922–9927.

Dum, R. P. and P. L. Strick (1991). "The origin of corticospinal projections from the premotor areas in the frontal lobe." Journal of Neuroscience 11(3): 667–689.

Dunn, W. (2001). "The sensations of everyday life: Empirical, theoretical, and pragmatic considerations." American Journal of Occupational Therapy 55(6): 608–620.

Earley, P. C. (1985). "Influence of information, choice and task complexity upon goal acceptance, performance, and personal goals." Journal of Applied Psychology 70(3): 481.

Eccles, J. C. (1968). "Physiology of nerve cells."

Edquist, J., C. M. Rudin–Brown and M. G. Lenné (2012). "The effects of on–street parking and road environment visual complexity on travel speed and reaction time." Accident Analysis & Prevention

45: 759–765.

Eisenbarth, H., L. J. Chang and T. D. Wager (2016). "Multivariate brain prediction of heart rate and skin conductance responses to social threat." Journal of Neuroscience 36(47): 11987–11998.

Elliott, D., J. Lyons, S. J. Hayes, J. J. Burkitt, J. W. Roberts, L. E. Grierson, S. Hansen and S. J. Bennett (2017). "The multiple process model of goal-directed reaching revisited." Neuroscience & Biobehavioral Reviews 72: 95–110.

Fahrer, M. (1981). "Interdependent and independent actions of the fingers." The hand 1: 399–403.

Fan, L., H. Li, J. Zhuo, Y. Zhang, J. Wang, L. Chen, Z. Yang, C. Chu, S. Xie and A. R. Laird (2016). "The human brainnetome atlas: a new brain atlas based on connectional architecture." Cerebral cortex 26(8): 3508–3526.

Farina, A. J., G. R. Wheaton and E. A. Fleishman (1971). Development of a taxonomy of human performance: The task characteristics approach to performance prediction, AMERICAN INSTITUTES FOR RESEARCH PITTSBURGH PA.

Feldman, A. G. (1986). "Once more on the equilibrium-point hypothesis (λ model) for motor control." Journal of motor behavior 18(1): 17–54.

Feldman, A. G. and M. F. Levin (2009). The equilibrium-point hypothesis–past, present and future. Progress in motor control, Springer: 699–726.

Feltz, D. L., D. M. Landers and B. J. Becker (1988). A revised meta-analysis of the mental practice literature on motor skill learning.

Ferber, R., L. R. Osternig, M. H. Woollacott, N. J. Wasielewski and J.-H. Lee (2002). "Reactive balance adjustments to unexpected perturbations during human walking." Gait & posture 16(3): 238–248.

Flannigan, J. C., R. Chua and E. K. Cressman (2016). "The rapid-chase theory does not extend to movement execution." Consciousness and Cognition 42: 75–92.

Fleishman, E. A. (1975). "Toward a taxonomy of human performance." American Psychologist 30(12): 1127.

Fornito, A., A. Zalesky and E. Bullmore (2016). Fundamentals of brain network analysis, Academic Press.

Fournier, L. R., G. F. Wilson and C. R. Swain (1999). "Electrophysiological, behavioral, and subjective indexes of workload when performing multiple tasks: manipulations of task difficulty and training." International Journal of Psychophysiology 31(2): 129-145.

Freedman, D. J. and G. Ibos (2018). "An integrative framework for sensory, motor, and cognitive functions of the posterior parietal cortex." Neuron 97(6): 1219-1234.

Frère, J. and F. Hug (2012). "Between-subject variability of muscle synergies during a complex motor skill." Frontiers in computational neuroscience 6: 99.

Freud, E., D. C. Plaut and M. Behrmann (2016). "‘What’is happening in the dorsal visual pathway." Trends in Cognitive Sciences 20(10): 773-784.

Friedman, J., V. Skm, V. M. Zatsiorsky and M. L. Latash (2009). "The sources of two components of variance: an example of multifinger cyclic force production tasks at different frequencies." Experimental Brain Research 196(2): 263-277.

Friedman, J., S. Varadhan, V. M. Zatsiorsky and M. L. Latash (2009). "The sources of two components of variance: an example of multifinger cyclic force production tasks at different frequencies." Experimental brain research 196(2): 263-277.

Friston, K. (2011). "What is optimal about motor control?" Neuron 72(3): 488-498.

Funato, T., S. Aoi, N. Tomita and K. Tsuchiya (2015). "Validating the feedback control of intersegmental coordination by fluctuation analysis of disturbed walking." Experimental Brain Research 233(5): 1421-1432.

Fuster, J. (2015). The prefrontal cortex, Academic Press.

Gallese, V., L. Fadiga, L. Fogassi and G. Rizzolatti (1996). "Action recognition in the premotor cortex." Brain 119(2): 593-609.

Geldard, F. A., R. O'Hehir and D. Gavens (1953). The human senses, Wiley New York.

Gentsch, A., A. Weber, M. Synofzik, G. Vosgerau and S. Schütz-Bosbach (2016). "Towards a common framework of grounded action cognition: Relating motor control, perception and cognition." Cognition 146: 81-89.

Georgopoulos, A. P. (2000). "Neural aspects of cognitive motor control." Current opinion in neurobiology 10(2): 238-241.

Gera, G., S. Freitas, M. Latash, K. Monahan, G. Schöner and J. Scholz (2010). "Motor abundance contributes to resolving multiple kinematic task constraints." Motor Control 14(1): 83-115.

Getchell, N. and J. Whitall (2003). "How do children coordinate simultaneous upper and lower extremity tasks? The development of dual motor task coordination." Journal of Experimental Child Psychology 85(2): 120-140.

Gielen, C. and J. C. Houk (1984). "Nonlinear viscosity of human wrist." Journal of Neurophysiology 52(3): 553-569.

Gordon, K. E., M. Wu, J. H. Kahn and B. D. Schmit (2010). "Feedback and feedforward locomotor adaptations to ankle-foot load in people with incomplete spinal cord injury." Journal of neurophysiology 104(3): 1325-1338.

Gorniak, S. L., V. M. Zatsiorsky and M. L. Latash (2007). "Hierarchies of synergies: an example of two-hand, multi-finger tasks." Experimental Brain Research 179(2): 167-180.

Grafton, S. T. (2010). "The cognitive neuroscience of prehension: recent developments." Experimental brain research 204(4): 475-491.

Grüsser, O.-J. (1995). On the history of the ideas of efference copy and reafference. Essays in the History of the Physiological Sciences, Brill Rodopi: 35-55.

Haeufle, D., S. Grimmer, K.-T. Kalveram and A. Seyfarth (2012). "Integration of intrinsic muscle properties, feed-forward and feedback signals for generating and stabilizing hopping." Journal of The Royal Society Interface 9(72): 1458-1469.

Haeufle, D. F., B. Schmortte, H. Geyer, R. Müller and S. Schmitt (2018). "The benefit of combining neuronal feedback and feed-forward control for robustness in step down perturbations of simulated human walking depends on the muscle function." Frontiers in computational neuroscience 12: 80.

Häger-Ross, C. and M. H. Schieber (2000). "Quantifying the independence of human finger movements: comparisons of digits, hands, and movement frequencies." Journal of Neuroscience 20(22): 8542-8550.

Haith, A. M. and J. W. Krakauer (2018). "The multiple effects of practice: skill, habit and reduced cognitive load." Current opinion in behavioral sciences 20: 196-201.

Hare, T. A., C. F. Camerer and A. Rangel (2009). "Self-control in decision-making involves modulation of the vmPFC valuation system." Science 324(5927): 646-648.

Hay, L. and C. Bard (1984). "The role of movement speed in learning a visuo-manual coordination in children." Psychological research 46(1-2): 177-186.

Hay, L. and C. Redon (1999). "Feedforward versus feedback control in children and adults subjected to a postural disturbance." Experimental Brain Research 125(2): 153-162.

Heitz, R. P. (2014). "The speed-accuracy tradeoff: history, physiology, methodology, and behavior." Frontiers in neuroscience 8: 150.

Heitz, R. P. and J. D. Schall (2012). "Neural mechanisms of speed-accuracy tradeoff." Neuron 76(3): 616-628.

Hemami, H. and Z. Moussavi (2014). "A model of the basal ganglia in voluntary movement and postural reactions." Computer methods in biomechanics and biomedical engineering 17(13): 1432-1446.

Herbort, O. and M. V. Butz (2012). "The continuous end-state comfort effect: weighted integration of multiple biases." Psychological research 76(3): 345-363.

Higashionna, T., R. Iwanaga, A. Tokunaga, A. Nakai, K. Tanaka, H. Nakane and G. Tanaka (2017). "Relationship between motor coordination, cognitive abilities, and academic achievement in Japanese children with neurodevelopmental disorders." Hong Kong Journal of Occupational Therapy 30(1): 49-55.

Ho, T., S. Brown, L. Van Maanen, B. U. Forstmann, E.-J.

Wagenmakers and J. T. Serences (2012). "The optimality of sensory processing during the speed–accuracy tradeoff." Journal of Neuroscience 32(23): 7992−8003.

Hogan, N. and D. Sternad (2007). "On rhythmic and discrete movements: reflections, definitions and implications for motor control." Experimental Brain Research 181(1): 13−30.

Höhne, A., C. Stark, G.−P. Brüggemann and A. Arampatzis (2011). "Effects of reduced plantar cutaneous afferent feedback on locomotor adjustments in dynamic stability during perturbed walking." Journal of biomechanics 44(12): 2194−2200.

Holper, L., M. Biallas and M. Wolf (2009). "Task complexity relates to activation of cortical motor areas during uni−and bimanual performance: a functional NIRS study." Neuroimage 46(4): 1105−1113.

Holper, L. and M. Wolf (2011). "Single−trial classification of motor imagery differing in task complexity: a functional near−infrared spectroscopy study." Journal of neuroengineering and rehabilitation 8(1): 34.

Hong, S., Y. Oh, D. Kim and B.−J. You (2013). "Real−time walking pattern generation method for humanoid robots by combining feedback and feedforward controller." IEEE transactions on industrial electronics 61(1): 355−364.

Horvitz, J. C. (2009). "Stimulus–response and response–outcome learning mechanisms in the striatum." Behavioural brain research 199(1): 129−140.

Hoshi, E. and J. Tanji (2000). "Integration of target and body−part information in the premotor cortex when planning action." Nature 408(6811): 466−470.

Houk, J. C. and S. P. Wise (1995). "Distributed modular architectures linking basal ganglia, cerebellum, and cerebral cortex: their role in planning and controlling action." Cerebral cortex 5(2): 95−110.

Hsu, J. (2009). Aging related differences in hand intrinsic and extrinsic muscles for hand dexterity: an MRI investigation.

Hu, D., D. Howard and L. Ren (2014). "Biomechanical analysis of the human finger extensor mechanism during isometric pressing."

PloS one 9(4): e94533.

Huang, S., B. Van Syoc, R. Yang, T. Kuehn, D. Smith and Q. Zhu (2020). "Using visual and/or kinesthetic information to stabilize intrinsic bimanual coordination patterns is a function of movement frequency." Psychological Research: 1-14.

Iacoboni, M., L. M. Koski, M. Brass, H. Bekkering, R. P. Woods, M.-C. Dubeau, J. C. Mazziotta and G. Rizzolatti (2001). "Reafferent copies of imitated actions in the right superior temporal cortex." Proceedings of the national academy of sciences 98(24): 13995-13999.

Ishibuchi, H. and Y. Nojima (2005). Accuracy-complexity tradeoff analysis by multiobjective rule selection. Proc. of ICDM 2005 Workshop on Computational Intelligence in Data Mining.

Ishii, K., N. Liang, R. Asahara, M. Takahashi and K. Matsukawa (2018). "Feedforward‐ and motor effort‐dependent increase in prefrontal oxygenation during voluntary one‐armed cranking." The Journal of Physiology 596(21): 5099-5118.

Jackson, J. H. (1873). On the localisation of movements in the brain, J. and A. Churchill.

Jacobs, J. V., J.-S. Lou, J. A. Kraakevik and F. B. Horak (2009). "The supplementary motor area contributes to the timing of the anticipatory postural adjustment during step initiation in participants with and without Parkinson's disease." Neuroscience 164(2): 877-885.

Jacobson, M. D., R. Raab, B. M. Fazeli, R. A. Abrams, M. J. Botte and R. L. Lieber (1992). "Architectural design of the human intrinsic hand muscles." The Journal of hand surgery 17(5): 804-809.

Jacobson, S., E. M. Marcus and S. Pugsley (2011). Neuroanatomy for the Neuroscientist, Springer.

Jarus, T. and T. Gutman (2001). "Effects of cognitive processes and task complexity on acquisition, retention, and transfer of motor skills." Canadian Journal of Occupational Therapy 68(5): 280-289.

Jenkins, I. H., R. E. Passingham and D. J. Brooks (1997). "The effect of movement frequency on cerebral activation: a positron emission tomography study." Journal of the neurological sciences 151(2): 195-205.

Jirsa, V. K. and J. Scott Kelso (2005). "The excitator as a minimal model for the coordination dynamics of discrete and rhythmic movement generation." Journal of motor behavior 37(1): 35-51.

Jo, H., C. Maenza, D. Good, X. Huang, J. Park, R. Sainburg and M. Latash (2016). "Effects of unilateral stroke on multi-finger synergies and their feed-forward adjustments." Neuroscience 319: 194-205.

Jo, H. J., S. Ambike, M. M. Lewis, X. Huang and M. L. Latash (2016). "Finger force changes in the absence of visual feedback in patients with Parkinson's disease." Clinical Neurophysiology 127(1): 684-692.

Jo, H. J., C. Maenza, D. C. Good, X. Huang, J. Park, R. L. Sainburg and M. L. Latash (2016). "Effects of unilateral stroke on multi-finger synergies and their feed-forward adjustments." Neuroscience 319: 194-205.

Jo, H. J., J. Park, M. M. Lewis, X. Huang and M. L. Latash (2015). "Prehension synergies and hand function in early-stage Parkinson's disease." Experimental brain research 233(2): 425-440.

Jones, E. and T. Powell (1970). "Connexions of the somatic sensory cortex of the rhesus monkey: III.—thalamic connexions." Brain 93(1): 37-56.

Jordan, M. I. and D. M. Wolpert (1999). Computational motor control, MIT Press Cambridge, MA.

Joukal, M. (2017). Anatomy of the human visual pathway. Homonymous visual field defects, Springer: 1-16.

Joyce, G., P. Rack and D. Westbury (1969). "The mechanical properties of cat soleus muscle during controlled lengthening and shortening movements." The Journal of physiology 204(2): 461-474.

Jueptner, M. and C. Weiller (1995). "does measurement of regional cerebral blood flow reflect synaptic activity? Implications for PET and fMRI." Neuroimage 2(2): 148.

Kandel, E. R., J. H. Schwartz, T. M. Jessell, D. o. Biochemistry, M. B. T. Jessell, S. Siegelbaum and A. Hudspeth (2000). Principles of neural science, McGraw–hill New York.

Kanekar, N. and A. S. Aruin (2014). "The effect of aging on anticipatory postural control." Experimental brain research 232(4): 1127–1136.

Kang, N., M. Shinohara, V. M. Zatsiorsky and M. L. Latash (2004). "Learning multi–finger synergies: an uncontrolled manifold analysis." Experimental Brain Research 157(3): 336–350.

Kao, P.–C. and D. P. Ferris (2005). "The effect of movement frequency on interlimb coupling during recumbent stepping." Motor control 9(2): 144–163.

Kapur, S., V. M. Zatsiorsky and M. L. Latash (2010). "Age–related changes in the control of finger force vectors." Journal of Applied Physiology 109(6): 1827–1841.

Kaufman, M. T., M. M. Churchland and K. V. Shenoy (2013). "The roles of monkey M1 neuron classes in movement preparation and execution." Journal of neurophysiology 110(4): 817–825.

Kawato, M. (1999). "Internal models for motor control and trajectory planning." Current opinion in neurobiology 9(6): 718–727.

Kim, J. A., J. C. Eliassen and J. N. Sanes (2005). "Movement quantity and frequency coding in human motor areas." Journal of neurophysiology 94(4): 2504–2511.

Kim, S. W., J. K. Shim, V. M. Zatsiorsky and M. L. Latash (2006). "Anticipatory adjustments of multi–finger synergies in preparation for self–triggered perturbations." Experimental brain research 174(4): 604–612.

Kim, S. W., J. K. Shim, V. M. Zatsiorsky and M. L. Latash (2008). "Finger inter–dependence: Linking the kinetic and kinematic variables." Human movement science 27(3): 408–422.

King, G. W., A. P. Bruetsch and J. T. Kevern (2013). "Slip–related characterization of gait kinetics: Investigation of pervious concrete as a slip–resistant walking surface." Safety Science 57: 52–59.

Klous, M., P. Mikulic and M. L. Latash (2011). "Two aspects of feedforward postural control: anticipatory postural adjustments and anticipatory synergy adjustments." Journal of neurophysiology 105(5): 2275–2288.

Klous, M., P. Mikulic and M. L. Latash (2012). "Early postural adjustments in preparation to whole–body voluntary sway." Journal of Electromyography and Kinesiology 22(1): 110–116.

Kluger, A. N. and A. DeNisi (1996). "The effects of feedback interventions on performance: A historical review, a meta–analysis, and a preliminary feedback intervention theory." Psychological bulletin 119(2): 254.

Koh, K., H. J. Kwon, Y. S. Park, T. Kiemel, R. H. Miller, Y. H. Kim, J.–H. Shin and J. K. Shim (2016). "Intra–auditory integration improves motor performance and synergy in an accurate multi–finger pressing task." Frontiers in Human Neuroscience 10: 260.

Komi, P. V. and C. Bosco (1978). "Muscles by men and women." Med Sci Sport 10: 261–265.

Kozlowski, S. W. and B. M. Hults (1986). "Joint moderation of the relation between task complexity and job performance for engineers." Journal of Applied Psychology 71(2): 196.

Krieglmeyer, R. and R. Deutsch (2010). "Comparing measures of approach–avoidance behaviour: The manikin task vs. two versions of the joystick task." Cognition and emotion 24(5): 810–828.

Krishnan, V., A. S. Aruin and M. L. Latash (2011). "Two stages and three components of the postural preparation to action." Experimental Brain Research 212(1): 47–63.

Krishnan, V. and S. Jaric (2010). "Effects of task complexity on coordination of inter–limb and within–limb forces in static bimanual manipulation." Motor control 14(4): 528–544.

Krukow, P., K. Jonak, H. Karakuła–Juchnowicz, A. Podkowiński, K. Jonak, M. Borys and M. Harciarek (2018). "Disturbed functional connectivity within the left prefrontal cortex and sensorimotor areas predicts impaired cognitive speed in patients with first–episode schizophrenia." Psychiatry Research: Neuroimaging 275: 28–35.

Kuboyama, N., T. Nabetani, K. Shibuya, K. Machida and T. Ogaki (2005). "Relationship between cerebral activity and movement frequency of maximal finger tapping." Journal of physiological anthropology and applied human science 24(3): 201-208.

Kuo, A. D. (2002). "The relative roles of feedforward and feedback in the control of rhythmic movements." Motor control 6(2): 129-145.

Kurata, K. (2005). "Activity properties and location of neurons in the motor thalamus that project to the cortical motor areas in monkeys." Journal of neurophysiology 94(1): 550-566.

Kurtzer, I. L. (2015). "Long-latency reflexes account for limb biomechanics through several supraspinal pathways." Frontiers in integrative neuroscience 8: 99.

Laguna, P. L. (2008). "Task complexity and sources of task-related information during the observational learning process." Journal of sports sciences 26(10): 1097-1113.

Lang, C. E. and M. H. Schieber (2004). "Human finger independence: limitations due to passive mechanical coupling versus active neuromuscular control." Journal of neurophysiology 92(5): 2802-2810.

Larson, G. E., C. R. Merritt and S. E. Williams (1988). "Information processing and intelligence: Some implications of task complexity." Intelligence 12(2): 131-147.

Latash, M. (2000). "There is no motor redundancy in human movements. There is motor abundance." Motor control 4(3): 259-261.

Latash, M. L. (2008). Neurophysiological basis of movement, Human Kinetics.

Latash, M. L. (2010). "Motor synergies and the equilibrium-point hypothesis." Motor control 14(3): 294-322.

Latash, M. L. (2012). "The bliss (not the problem) of motor abundance (not redundancy)." Experimental brain research 217(1): 1-5.

Latash, M. L., S. Gorniak and V. M. Zatsiorsky (2008). "Hierarchies of synergies in human movements." Kinesiology: International journal of fundamental and applied kinesiology 40(1.): 29–38.

Latash, M. L. and X. Huang (2015). "Neural control of movement stability: Lessons from studies of neurological patients." Neuroscience 301: 39–48.

Latash, M. L., J. P. Scholz and G. Schöner (2002). "Motor control strategies revealed in the structure of motor variability." Exercise and sport sciences reviews 30(1): 26–31.

Latash, M. L., J. P. Scholz and G. Schöner (2007). "Toward a new theory of motor synergies." Motor control 11(3): 276–308.

Latash, M. L. and V. M. Zatsiorsky (2009). Multi–finger prehension: control of a redundant mechanical system. Progress in Motor Control, Springer: 597–618.

Laurienti, P. J., J. H. Burdette, J. A. Maldjian and M. T. Wallace (2006). "Enhanced multisensory integration in older adults." Neurobiology of aging 27(8): 1155–1163.

Leigh, R. J. and D. S. Zee (2015). The neurology of eye movements, OUP USA.

Leisman, G., A. A. Moustafa and T. Shafir (2016). "Thinking, walking, talking: integratory motor and cognitive brain function." Frontiers in public health 4: 94.

Lestienne, F. G., F. Thullier, P. Archambault, M. F. Levin and A. G. Feldman (2000). "Multi–muscle control of head movements in monkeys: the referent configuration hypothesis." Neuroscience Letters 283(1): 65–68.

Lew, S. E., H. G. Rey, D. A. Gutnisky and B. S. Zanutto (2008). "Differences in prefrontal and motor structures learning dynamics depend on task complexity: A neural network model." Neurocomputing 71(13–15): 2782–2793.

Li, S., M. L. Latash and V. M. Zatsiorsky (2003). "Finger interaction during multi–finger tasks involving finger addition and removal." Experimental brain research 150(2): 230–236.

Li, T., D. Wang, C. Peng, C. Yu and Y. Zhang (2018). "Speed–accuracy tradeoff of fingertip force control with visual/audio/haptic feedback." International Journal of Human–Computer Studies 110: 33–44.

Li, Z.−M., S. Dun, D. A. Harkness and T. L. Brininger (2004). "Motion enslaving among multiple fingers of the human hand." Motor control 8(1): 1−15.

Li, Z.−M., V. Zatsiorsky and M. Latash (2001). "The effect of finger extensor mechanism on the flexor force during isometric tasks." Journal of biomechanics 34(8): 1097−1102.

Li, Z.−M., V. M. Zatsiorsky, M. L. Latash and N. Bose (2002). "Anatomically and experimentally based neural networks modeling force coordination in static multi−finger tasks." Neurocomputing 47(1): 259−275.

Li, Z. N., M. L. Latash, K. M. Newell and V. M. Zatsiorsky (1998). "Motor redundancy during maximal voluntary contraction in four−finger tasks." Experimental Brain Research 122(1): 71−78.

Liefooghe, B. and F. Verbruggen (2019). "On the Assimilation of Instructions: Stimulus−response Associations are Implemented but not Stimulus−task Associations." Journal of cognition 2(1).

Lien, M.−C. and R. W. Proctor (2002). "Stimulus−response compatibility and psychological refractory period effects: Implications for response selection." Psychonomic bulletin & review 9(2): 212−238.

Lieu, J. (2008). The effects of finger movement conditions and speed on finger interdependency.

Liu, A. T., B. L. Liu, L. X. Lu, G. Chen, D. Z. Yu, L. Zhu, R. Guo, R. S. Dang and H. Jiang (2014). "Architectural properties of the neuromuscular compartments in selected forearm skeletal muscles." Journal of anatomy 225(1): 12−18.

Liu, P. and Z. Li (2012). "Task complexity: A review and conceptualization framework." International Journal of Industrial Ergonomics 42(6): 553−568.

Liu, Z., M. J. Sinclair, A. Acero, X. D. Huang, J. G. Droppo, L. Deng, Z. Zhang and Y. Zheng (2008). Method and apparatus for multi−sensory speech enhancement, Google Patents.

Locke, E. A., E. Frederick, C. Lee and P. Bobko (1984). "Effect of self−efficacy, goals, and task strategies on task performance." Journal of applied psychology 69(2): 241.

Lu, C.−H. and R. W. Proctor (1995). "The influence of irrelevant location information on performance: A review of the Simon and spatial Stroop effects." Psychonomic bulletin & review 2(2): 174−207.

Ma, H.−i. and C. A. Trombly (2004). "Effects of task complexity on reaction time and movement kinematics in elderly people." American Journal of Occupational Therapy 58(2): 150−158.

MacDonald, A. W., J. D. Cohen, V. A. Stenger and C. S. Carter (2000). "Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control." Science 288(5472): 1835−1838.

Macefield, V. G. (2013). "Discharge rates and discharge variability of muscle spindle afferents in human chronic spinal cord injury." Clinical neurophysiology 124(1): 114−119.

MacKenzie, C. L. and T. Iberall (1994). The grasping hand, Elsevier.

Madarsara, M. A. and R. Rahimy (2015). "Examining the effect of task complexity and sequence on speaking ability of Iranian EFL learners." International Journal of Applied Linguistics and English Literature 4(1): 247−254.

Maes, C., S. P. Swinnen, G. Albouy, S. Sunaert, J. Gooijers, S. Chalavi and L. Pauwels (2020). "The role of PMd in task complexity: functional connectivity is modulated by motor learning and age." Neurobiology of Aging.

Manes, F., B. Sahakian, L. Clark, R. Rogers, N. Antoun, M. Aitken and T. Robbins (2002). "Decision‐making processes following damage to the prefrontal cortex." Brain 125(3): 624−639.

Markowitz, D. A., C. E. Curtis and B. Pesaran (2015). "Multiple component networks support working memory in prefrontal cortex." Proceedings of the National Academy of Sciences 112(35): 11084−11089.

Martin, J. R., M. L. Latash and V. M. Zatsiorsky (2009). "Interaction of finger enslaving and error compensation in multiple finger force production." Experimental brain research 192(2): 293−298.

Martin, J. R., A. V. Terekhov, M. L. Latash and V. M. Zatsiorsky (2013). "Optimization and variability of motor behavior in multifinger tasks: what variables does the brain use?" Journal of motor behavior 45(4): 289−305.

Martin, V., J. P. Scholz and G. Schöner (2009). "Redundancy, self−motion, and motor control." Neural computation 21(5): 1371−1414.

Mattar, A. A. and P. L. Gribble (2005). "Motor learning by observing." Neuron 46(1): 153−160.

Matthews, P. (1959). "A study of certain factors influencing the stretch reflex of the decerebrate cat." The Journal of physiology 147(3): 547.

Matthews, P. B. (1991). "The human stretch reflex and the motor cortex." Trends in neurosciences 14(3): 87−91.

McMillan, S., R. B. Ivry and W. D. Byblow (2006). "Corticomotor excitability during a choice−hand reaction time task." Experimental brain research 172(2): 230−245.

Meijer, D., S. Veselič, C. Calafiore and U. Noppeney (2019). "Integration of audiovisual spatial signals is not consistent with maximum likelihood estimation." Cortex 119: 74−88.

Meister, I., T. Krings, H. Foltys, B. Boroojerdi, M. Müller, R. Töpper and A. Thron (2005). "Effects of long‐term practice and task complexity in musicians and nonmusicians performing simple and complex motor tasks: Implications for cortical motor organization." Human brain mapping 25(3): 345−352.

Messier, J., S. Adamovich, M. Berkinblit, E. Tunik and H. Poizner (2003). "Influence of movement speed on accuracy and coordination of reaching movements to memorized targets in three−dimensional space in a deafferented subject." Experimental Brain Research 150(4): 399−416.

Miall, R. C. and D. M. Wolpert (1996). "Forward models for physiological motor control." Neural networks 9(8): 1265−1279.

Mihara, M., I. Miyai, M. Hatakenaka, K. Kubota and S. Sakoda (2008). "Role of the prefrontal cortex in human balance control." Neuroimage 43(2): 329−336.

Miller, B. L. and J. L. Cummings (2017). The human frontal lobes: Functions and disorders, Guilford Publications.

Miller, E. K. and J. D. Cohen (2001). "An integrative theory of prefrontal cortex function." Annual review of neuroscience 24(1): 167-202.

Milton, J. G., T. Insperger, W. Cook, D. M. Harris and G. Stepan (2018). "Microchaos in human postural balance: Sensory dead zones and sampled time-delayed feedback." Physical review E 98(2): 022223.

Mohandas Nair, P., T. George Hornby and A. Louis Behrman (2012). "Minimal detectable change for spatial and temporal measurements of gait after incomplete spinal cord injury." Topics in spinal cord injury rehabilitation 18(3): 273-281.

Mohapatra, S. and A. S. Aruin (2013). "Static and dynamic visual cues in feed-forward postural control." Experimental brain research 224(1): 25-34.

Monjo, F. and N. Forestier (2014). "Unexperienced mechanical effects of muscular fatigue can be predicted by the Central Nervous System as revealed by anticipatory postural adjustments." Experimental brain research 232(9): 2931-2943.

Morton, S. M. and A. J. Bastian (2006). "Cerebellar contributions to locomotor adaptations during splitbelt treadmill walking." Journal of Neuroscience 26(36): 9107-9116.

Mtui, E., G. Gruener and P. Dockery (2015). Fitzgerald's Clinical Neuroanatomy and Neuroscience E-Book, Elsevier Health Sciences.

Müller, R., D. F. B. Häufle and R. Blickhan (2015). "Preparing the leg for ground contact in running: the contribution of feed-forward and visual feedback." Journal of Experimental Biology 218(3): 451-457.

Murray, M. M. and M. T. Wallace (2011). The neural bases of multisensory processes, CRC Press.

Mussini, E., M. Berchicci, V. Bianco, R. Perri, F. Quinzi and F. Di Russo (2020). "Effect of task complexity on motor and cognitive preparatory brain activities." International Journal of Psychophysiology 159: 11-16.

Nafcha, O., E. T. Higgins and B. Eitam (2016). Control feedback as the motivational force behind habitual behavior. Progress in brain research, Elsevier. 229: 49-68.

Naik, G. R. and H. T. Nguyen (2014). "Nonnegative matrix factorization for the identification of EMG finger movements: Evaluation using matrix analysis." IEEE journal of biomedical and health informatics 19(2): 478-485.

Neely, R. M., A. C. Koralek, V. R. Athalye, R. M. Costa and J. M. Carmena (2018). "Volitional modulation of primary visual cortex activity requires the basal ganglia." Neuron 97(6): 1356-1368. e1354.

Newell, K. and L. G. Carlton (1988). "Force variability in isometric responses." Journal of Experimental Psychology: Human Perception and Performance 14(1): 37.

Nieder, A. and K. Merten (2007). "A labeled-line code for small and large numerosities in the monkey prefrontal cortex." Journal of Neuroscience 27(22): 5986-5993.

Niutanen, U., T. Harra, A. Lano and M. Metsäranta (2020). "Systematic review of sensory processing in preterm children reveals abnormal sensory modulation, somatosensory processing and sensory - based motor processing." Acta Paediatrica 109(1): 45-55.

Oh, S.-Y., R. Boegle, M. Ertl, T. Stephan and M. Dieterich (2018). "Multisensory vestibular, vestibular-auditory, and auditory network effects revealed by parametric sound pressure stimulation." Neuroimage 176: 354-363.

Oh, S.-Y., R. Boegle, M. Ertl, P. Zu Eulenburg, T. Stephan and M. Dieterich (2017). "Auditory induced vestibular (otolithic) processing revealed by an independent component analysis: an fMRI parametric analysis." Journal of Neurology 264(1): 23-25.

Ohmae, S., J. Kunimatsu and M. Tanaka (2017). "Cerebellar roles in self-timing for sub-and supra-second intervals." Journal of Neuroscience 37(13): 3511-3522.

Olafsdottir, H., N. Yoshida, V. M. Zatsiorsky and M. L. Latash (2005). "Anticipatory covariation of finger forces during self-paced and reaction time force production." Neuroscience letters 381(1-2):

92–96.

Olafsdottir, H. B., S. W. Kim, V. M. Zatsiorsky and M. L. Latash (2008). "Anticipatory synergy adjustments in preparation to self–triggered perturbations in elderly individuals." Journal of applied biomechanics 24(2): 175–179.

Oldfield, R. C. (1971). "The assessment and analysis of handedness: the Edinburgh inventory." Neuropsychologia 9(1): 97–113.

Oliveira, M. A., J. K. Shim, J. F. Loss, R. D. Petersen and J. E. Clark (2006). "Effect of kinetic redundancy on hand digit control in children with DCD." Neuroscience Letters 410(1): 42–46.

Olivier, E., M. Davare, M. Andres and L. Fadiga (2007). "Precision grasping in humans: from motor control to cognition." Current opinion in neurobiology 17(6): 644–648.

Oostwoud Wijdenes, L., R. B. Ivry and P. M. Bays (2016). "Competition between movement plans increases motor variability: evidence of a shared resource for movement planning." Journal of neurophysiology 116(3): 1295–1303.

Orasanu, J. and T. Connolly (1993). "The reinvention of decision making." Decision making in action: Models and methods 1: 3–20.

Ostry, D. J. and P. L. Gribble (2016). "Sensory plasticity in human motor learning." Trends in neurosciences 39(2): 114–123.

Palmer, E. and P. Ashby (1992). "Corticospinal projections to upper limb motoneurones in humans." The Journal of physiology 448(1): 397–412.

Palva, J. M. and S. Palva (2011). Roles of multiscale brain activity fluctuations in shaping the variability and dynamics of psychophysical performance. Progress in brain research, Elsevier. 193: 335–350.

Park, J., D.–W. Han and J. K. Shim (2015). "Effect of resistance training of the wrist joint muscles on multi–digit coordination." Perceptual and motor skills 120(3): 816–840.

Park, J., M. M. Lewis, X. Huang and M. L. Latash (2013). "Effects of olivo–ponto–cerebellar atrophy (OPCA) on finger interaction and coordination." Clinical Neurophysiology 124(5): 991–998.

Park, J., M. M. Lewis, X. Huang and M. L. Latash (2014).

"Dopaminergic modulation of motor coordinaton in Parkinson's disease." Parkinsonism & related disorders 20(1): 64-68.

Park, J., Y.-H. Wu, M. M. Lewis, X. Huang and M. L. Latash (2012). "Changes in multifinger interaction and coordination in Parkinson's disease." Journal of neurophysiology 108(3): 915-924.

Park, J. and D. Xu (2017). "Multi-finger interaction and synergies in finger flexion and extension force production." Frontiers in human neuroscience 11: 318.

Partridge, P. (1965). "Cyclic twinning in fatigued close-packed hexagonal metals." The Philosophical Magazine: A Journal of Theoretical Experimental and Applied Physics 12(119): 1043-1054.

Patla, A. E. (2004). "Adaptive human locomotion: influence of neural, biological and mechanical factors on control mechanisms." Clinical disorders of balance, posture and gait 2.

Patlak, C. S. and R. G. Blasberg (1985). "Graphical evaluation of blood-to-brain transfer constants from multiple-time uptake data. Generalizations." Journal of Cerebral Blood Flow & Metabolism 5(4): 584-590.

Paus, T. (2001). "Primate anterior cingulate cortex: where motor control, drive and cognition interface." Nature reviews neuroscience 2(6): 417-424.

Paus, T., L. Koski, Z. Caramanos and C. Westbury (1998). "Regional differences in the effects of task difficulty and motor output on blood flow response in the human anterior cingulate cortex: a review of 107 PET activation studies." Neuroreport 9(9): R37-R47.

Petersson, P., A. Waldenström, C. Fåhraeus and J. Schouenborg (2003). "Spontaneous muscle twitches during sleep guide spinal self-organization." Nature 424(6944): 72-75.

Petryński, W. (2010). "FEEDFORWARD, FEEDBACK AND UCM IN MOTOR CONTROL IN HUMANS." Ovidius University Annals, Series Physical Education & Sport/Science, Movement & Health 10(2).

Pfeuffer, C. U., K. Moutsopoulou, F. Waszak and A. Kiesel (2018). "Multiple priming instances increase the impact of practice-based but not verbal code-based stimulus-response associations." Acta psychologica 184: 100-109.

Piantino, J., J. Burdick, D. Goldberg, R. Langer and L. Benowitz (2006). "An injectable, biodegradable hydrogel for trophic factor delivery enhances axonal rewiring and improves performance after spinal cord injury." Experimental neurology 201(2): 359-367.

Piscitelli, D., A. Falaki, S. Solnik and M. L. Latash (2017). "Anticipatory postural adjustments and anticipatory synergy adjustments: preparing to a postural perturbation with predictable and unpredictable direction." Experimental brain research 235(3): 713-730.

Plamondon, R. and A. M. Alimi (1997). "Speed/accuracy trade-offs in target-directed movements." Behavioral and brain sciences 20(2): 279-303.

Powell, D. W., B. Szekely, S. E. Blackmore, A. Nelson, A. Schallert, D. B. Lester and M. Puppa (2018). "Effects of sampling rate and movement frequency on entropic measures of regularity." Journal of Nature and Science 4(5): e504.

Prescott, S. A. and S. Ratté (2017). Somatosensation and pain. Conn's Translational Neuroscience, Elsevier: 517-539.

Preuss, T. M. and P. S. Goldman‐Rakic (1991). "Myelo‐and cytoarchitecture of the granular frontal cortex and surrounding regions in the strepsirhine primate Galago and the anthropoid primate Macaca." Journal of Comparative Neurology 310(4): 429-474.

Pruszynski, J. A., I. Kurtzer and S. H. Scott (2011). "The long-latency reflex is composed of at least two functionally independent processes." Journal of neurophysiology 106(1): 449-459.

Radach, R., J. Hyona and H. Deubel (2003). The mind's eye: Cognitive and applied aspects of eye movement research, Elsevier.

Rana, M., M. S. Yani, S. Asavasopon, B. E. Fisher and J. J. Kutch (2015). "Brain connectivity associated with muscle synergies in humans." Journal of Neuroscience 35(44): 14708–14716.

Ranganathan, R. and K. M. Newell (2008). "Motor synergies: feedback and error compensation within and between trials." Experimental brain research 186(4): 561–570.

Ranganathan, R. and K. M. Newell (2009). "Influence of augmented feedback on coordination strategies." Journal of motor behavior 41(4): 317–330.

Reader, A. T. and H. H. Ehrsson (2019). "Weakening the subjective sensation of own hand ownership does not interfere with rapid finger movements." PloS one 14(10): e0223580.

Redgrave, P., M. Rodriguez, Y. Smith, M. C. Rodriguez–Oroz, S. Lehericy, H. Bergman, Y. Agid, M. R. DeLong and J. A. Obeso (2010). "Goal–directed and habitual control in the basal ganglia: implications for Parkinson's disease." Nature Reviews Neuroscience 11(11): 760–772.

Rinkenauer, G., A. Osman, R. Ulrich, H. Müller–Gethmann and S. Mattes (2004). "On the locus of speed–accuracy trade–off in reaction time: inferences from the lateralized readiness potential." Journal of Experimental Psychology: General 133(2): 261.

Rissman, J., A. Gazzaley and M. D'Esposito (2004). "Measuring functional connectivity during distinct stages of a cognitive task." Neuroimage 23(2): 752–763.

Rizzolatti, G. and G. Luppino (2001). "The cortical motor system." Neuron 31(6): 889–901.

Robinson, P. and R. Gilabert (2007). "Task complexity, the Cognition Hypothesis and second language learning and performance." International Review of Applied Linguistics in Language Teaching 45(3): 161–176.

Rodieck, R. (1979). "Visual pathways." Annual Review of Neuroscience 2(1): 193–225.

Ronsse, R., R. C. Miall and S. P. Swinnen (2009). "Multisensory integration in dynamical behaviors: maximum likelihood estimation across bimanual skill learning." Journal of Neuroscience 29(26): 8419-8428.

Rosenbaum, D. A., C. M. van Heugten and G. E. Caldwell (1996). "From cognition to biomechanics and back: The end-state comfort effect and the middle-is-faster effect." Acta psychologica 94(1): 59-85.

Sabes, P. N. (2000). "The planning and control of reaching movements." Current opinion in neurobiology 10(6): 740-746.

Sadato, N., G. Campbell, V. Ibanez, M.-P. Deiber and M. Hallett (1996). "Complexity affects regional cerebral blood flow change during sequential finger movements." Journal of Neuroscience 16(8): 2693-2700.

Sadato, N., V. Ibañez, G. Campbell, M.-P. Deiber, D. Le Bihan and M. Hallett (1997). "Frequency-dependent changes of regional cerebral blood flow during finger movements: functional MRI compared to PET." Journal of Cerebral Blood Flow & Metabolism 17(6): 670-679.

Sarabon, N., G. Markovic, P. Mikulic and M. L. Latash (2013). "Bilateral synergies in foot force production tasks." Experimental brain research 227(1): 121-130.

Schaal, S., D. Sternad, R. Osu and M. Kawato (2004). "Rhythmic arm movement is not discrete." Nature neuroscience 7(10): 1136-1143.

Schieber, M. H. (1990). "How might the motor cortex individuate movements?" Trends in neurosciences 13(11): 440-445.

Schieber, M. H. and L. S. Hibbard (1993). "How somatotopic is the motor cortex hand area?" Science 261(5120): 489-492.

Schieber, M. H. and M. J. J. o. A. P. Santello (2004). "Hand function: peripheral and central constraints on performance." 96(6): 2293-2300.

Scholkmann, F., S. Kleiser, A. J. Metz, R. Zimmermann, J. M. Pavia, U. Wolf and M. Wolf (2014). "A review on continuous wave functional near-infrared spectroscopy and imaging instrumentation and methodology." Neuroimage 85: 6-27.

Scholz, J. P., F. Danion, M. L. Latash and G. SchoÈner (2002).

"Understanding finger coordination through analysis of the structure of force variability." Biological cybernetics 86(1): 29-39.

Scholz, J. P., N. Kang, D. Patterson and M. L. Latash (2003). "Uncontrolled manifold analysis of single trials during multi-finger force production by persons with and without Down syndrome." Experimental Brain Research 153(1): 45-58.

Scholz, J. P. and G. Schöner (1999). "The uncontrolled manifold concept: identifying control variables for a functional task." Experimental brain research 126(3): 289-306.

Scholz, J. P. and G. Schöner (2014). Use of the uncontrolled manifold (UCM) approach to understand motor variability, motor equivalence, and self-motion. Progress in motor control, Springer: 91-100.

Scott Jr, W. and J. Erskine (1980). "The effects of variations in task design and monetary reinforcers on task behavior." Organizational Behavior and Human Performance 25(3): 311-335.

Scott, S. H. (2004). "Optimal feedback control and the neural basis of volitional motor control." Nature Reviews Neuroscience 5(7): 532-545.

Seidler, R., D. Noll and G. Thiers (2004). "Feedforward and feedback processes in motor control." Neuroimage 22(4): 1775-1783.

Sengupta, J. N. (2009). Visceral pain: the neurophysiological mechanism. Sensory Nerves, Springer: 31-74.

Shah, P. K., Y. Gerasimenko, A. Shyu, I. Lavrov, H. Zhong, R. R. Roy and V. R. Edgerton (2012). "Variability in step training enhances locomotor recovery after a spinal cord injury." European Journal of Neuroscience 36(1): 2054-2062.

Shapkova, E. Y., A. L. Shapkova, S. R. Goodman, V. M. Zatsiorsky and M. L. Latash (2008). "Do synergies decrease force variability? A study of single-finger and multi-finger force production." Experimental Brain Research 188(3): 411-425.

Sherman, S. M. (2006). "Thalamus." Scholarpedia 1(9): 1583.

Shim, H., J. Y. Jang, J. W. Kim, H. Ryu, P. Y. Jung, S. Kim, H. Y.

Kwon, K. M. Kim, H. Chung and K. S. Bae (2018). "Effectiveness and postoperative wound infection of preperitoneal pelvic packing in patients with hemodynamic instability caused by pelvic fracture." PloS one 13(11): e0206991.

Shim, J. K., M. L. Latash and V. M. Zatsiorsky (2003). "Prehension synergies: trial–to–trial variability and hierarchical organization of stable performance." Experimental Brain Research 152(2): 173–184.

Shim, J. K., B. S. Lay, V. M. Zatsiorsky and M. L. Latash (2004). "Age–related changes in finger coordination in static prehension tasks." Journal of Applied Physiology 97(1): 213–224.

Shim, J. K., H. Olafsdottir, V. M. Zatsiorsky and M. L. Latash (2005). "The emergence and disappearance of multi–digit synergies during force–production tasks." Experimental Brain Research 164(2): 260–270.

Shim, J. K., M. A. Oliveira, J. Hsu, J. Huang, J. Park and J. E. Clark (2007). "Hand digit control in children: age–related changes in hand digit force interactions during maximum flexion and extension force production tasks." Experimental brain research 176(2): 374.

Shim, J. K., J. Park, V. M. Zatsiorsky and M. L. Latash (2006). "Adjustments of prehension synergies in response to self–triggered and experimenter–triggered load and torque perturbations." Experimental brain research 175(4): 641–653.

Shin, J., J. Kwon, J. Choi and C.–H. Im (2017). "Performance enhancement of a brain–computer interface using high–density multi–distance NIRS." Scientific reports 7(1): 1–10.

Shinohara, M., S. Li, N. Kang, V. M. Zatsiorsky and M. L. Latash (2003). "Effects of age and gender on finger coordination in MVC and submaximal force–matching tasks." Journal of applied physiology 94(1): 259–270.

Shiratori, T. and M. L. Latash (2001). "Anticipatory postural adjustments during load catching by standing subjects." Clinical neurophysiology 112(7): 1250–1265.

Shirinbayan, S. I., A. M. Dreyer and J. W. Rieger (2019). "Cortical and subcortical areas involved in the regulation of reach movement speed in the human brain: An fMRI study." Human brain mapping 40(1): 151-162.

Sigrist, R., G. Rauter, R. Riener and P. Wolf (2013). "Augmented visual, auditory, haptic, and multimodal feedback in motor learning: a review." Psychonomic bulletin & review 20(1): 21-53.

Singh, T., V. SKM, V. M. Zatsiorsky and M. L. Latash (2010). "Fatigue and motor redundancy: adaptive increase in finger force variance in multi-finger tasks." Journal of neurophysiology 103(6): 2990-3000.

Slifkin, A. B., D. E. Vaillancourt and K. M. Newell (2000). "Intermittency in the control of continuous force production." Journal of Neurophysiology 84(4): 1708-1718.

Sousa, A. S., A. Silva and R. Santos (2015). "Ankle anticipatory postural adjustments during gait initiation in healthy and post-stroke subjects." Clinical Biomechanics 30(9): 960-965.

Speier, C. (2006). "The influence of information presentation formats on complex task decision-making performance." International Journal of Human-Computer Studies 64(11): 1115-1131.

Spidalieri, G., L. Busby and Y. Lamarre (1983). "Fast ballistic arm movements triggered by visual, auditory, and somesthetic stimuli in the monkey. II. Effects of unilateral dentate lesion on discharge of precentral cortical neurons and reaction time." Journal of Neurophysiology 50(6): 1359-1379.

St-Onge, N. and A. G. Feldman (2004). "Referent configuration of the body: a global factor in the control of multiple skeletal muscles." Experimental brain research 155(3): 291-300.

Standage, D., G. Blohm and M. C. Dorris (2014). "On the neural implementation of the speed-accuracy trade-off." Frontiers in Neuroscience 8: 236.

Stanley, E. F. (1981). "Sensory and motor nerve conduction velocities and the latency of the H reflex during growth of the rat." Experimental neurology 71(3): 497-506.

Stegemöller, E. L., T. Simuni and C. MacKinnon (2009). "Effect of movement frequency on repetitive finger movements in patients with Parkinson's disease." Movement Disorders 24(8): 1162-1169.

Stenneken, P., W. Prinz, J. Cole, J. Paillard and G. Aschersleben (2006). "The effect of sensory feedback on the timing of movements: evidence from deafferented patients." Brain research 1084(1): 123-131.

Sternad, D. and W. J. Dean (2003). "Rhythmic and discrete elements in multi-joint coordination." Brain research 989(2): 152-171.

Sternad, D., W. J. Dean and S. Schaal (2000). "Interaction of rhythmic and discrete pattern generators in single-joint movements." Human Movement Science 19(4): 627-664.

Stoodley, C. J. and J. D. Schmahmann (2009). "Functional topography in the human cerebellum: a meta-analysis of neuroimaging studies." Neuroimage 44(2): 489-501.

Suzuki, M., I. Miyai, T. Ono, I. Oda, I. Konishi, T. Kochiyama and K. Kubota (2004). "Prefrontal and premotor cortices are involved in adapting walking and running speed on the treadmill: an optical imaging study." Neuroimage 23(3): 1020-1026.

Svoboda, K. and N. Li (2018). "Neural mechanisms of movement planning: motor cortex and beyond." Current opinion in neurobiology 49: 33-41.

Taga, G. (1995). "A model of the neuro-musculo-skeletal system for human locomotion." Biological cybernetics 73(2): 97-111.

Takahashi, C. D., D. Nemet, C. M. Rose-Gottron, J. K. Larson, D. M. Cooper and D. J. Reinkensmeyer (2006). "Effect of muscle fatigue on internal model formation and retention during reaching with the arm." Journal of applied physiology 100(2): 695-706.

Tanaka, M. (2007). "Cognitive signals in the primate motor thalamus predict saccade timing." Journal of Neuroscience 27(44): 12109-12118.

Taylor, J. A. and K. A. Thoroughman (2008). "Motor adaptation scaled by the difficulty of a secondary cognitive task." PLoS One 3(6): e2485.

Thiruvady, D. R., N. Georgiou-Karistianis, G. F. Egan, S. Ray, A.

Sritharan, M. Farrow, A. Churchyard, P. Chua, J. L. Bradshaw and T.-L. Brawn (2007). "Functional connectivity of the prefrontal cortex in Huntington's disease." Journal of Neurology, Neurosurgery & Psychiatry 78(2): 127-133.

Tittelbach, D., L. Fields and A. M. Alvero (2008). "Effects of performance feedback on typing speed and accuracy." Journal of Organizational Behavior Management 27(4): 29-52.

Togo, S. and H. Imamizu (2016). "Anticipatory synergy adjustments reflect individual performance of feedforward force control." Neuroscience Letters 632: 192-198.

Turvey, M. T. (1990). "Coordination." American psychologist 45(8): 938.

Ungerleider, L. G. (1982). "Two cortical visual systems." Analysis of visual behavior: 549-586.

Uylings, H. B., H. J. Groenewegen and B. Kolb (2003). "Do rats have a prefrontal cortex?" Behavioural brain research 146(1-2): 3-17.

Vahdat, S., M. Darainy, T. E. Milner and D. J. Ostry (2011). "Functionally specific changes in resting-state sensorimotor networks after motor learning." Journal of Neuroscience 31(47): 16907-16915.

Vaillancourt, D. E. and D. M. Russell (2002). "Temporal capacity of short-term visuomotor memory in continuous force production." Experimental brain research 145(3): 275-285.

van Beek, N., D. F. Stegeman, J. C. van den Noort, D. H. Veeger and H. Maas (2018). "Activity patterns of extrinsic finger flexors and extensors during movements of instructed and non-instructed fingers." Journal of Electromyography and Kinesiology 38: 187-196.

Van Donkelaar, P. and I. Franks (1991). "The effects of changing movement velocity and complexity on response preparation: evidence from latency, kinematic, and EMG measures." Experimental Brain Research 83(3): 618-632.

Van Horn, J. D., S. T. Grafton and M. B. Miller (2008). "Individual variability in brain activity: a nuisance or an opportunity?" Brain imaging and behavior 2(4): 327.

Verstynen, T., J. Diedrichsen, N. Albert, P. Aparicio and R. B. Ivry (2005). "Ipsilateral motor cortex activity during unimanual hand movements relates to task complexity." Journal of neurophysiology 93(3): 1209–1222.

Wallis, J. D. (2007). "Orbitofrontal cortex and its contribution to decision–making." Annu. Rev. Neurosci. 30: 31–56.

Wang, Y. and G. Ruhe (2007). "The cognitive process of decision making." International Journal of Cognitive Informatics and Natural Intelligence (IJCINI) 1(2): 73–85.

Wang, Y., K. Watanabe and T. Asaka (2016). "Aging effect on muscle synergies in stepping forth during a forward perturbation." European Journal of Applied Physiology: 1–11.

Watemberg, N., N. Waiserberg, L. Zuk and T. Lerman - Sagie (2007). "Developmental coordination disorder in children with attention - deficit–hyperactivity disorder and physical therapy intervention." Developmental Medicine & Child Neurology 49(12): 920–925.

Wei, D., J. Yang, W. Li, K. Wang, Q. Zhang and J. Qiu (2014). "Increased resting functional connectivity of the medial prefrontal cortex in creativity by means of cognitive stimulation." Cortex 51: 92–102.

Westendorp, M., E. Hartman, S. Houwen, J. Smith and C. Visscher (2011). "The relationship between gross motor skills and academic achievement in children with learning disabilities." Research in developmental disabilities 32(6): 2773–2779.

Wickens, C. D. and J. S. McCarley (2007). Applied attention theory, CRC press.

Wilmut, K. and M. Byrne (2014). "Grip selection for sequential movements in children and adults with and without Developmental Coordination Disorder." Human movement science 36: 272–284.

Winstein, C. J., S. T. Grafton and P. S. Pohl (1997). "Motor task difficulty and brain activity: investigation of goal–directed reciprocal aiming using positron emission tomography." Journal of Neurophysiology 77(3): 1581-1594.

Wolf, R. C., M. M. Plichta, F. Sambataro, A. J. Fallgatter, C. Jacob, K. P. Lesch, M. J. Herrmann, C. Schönfeldt‑Lecuona, B. J. Connemann and G. Grön (2009). "Regional brain activation changes and abnormal functional connectivity of the ventrolateral prefrontal cortex during working memory processing in adults with attention‑deficit/hyperactivity disorder." Human brain mapping 30(7): 2252-2266.

Wolff, P. H., K. Kotwica and M. Obregon (1998). "The development of interlimb coordination during bimanual finger tapping." International Journal of Neuroscience 93(1-2): 7-27.

Wolpert, D. M. and M. Kawato (1998). "Multiple paired forward and inverse models for motor control." Neural networks 11(7-8): 1317-1329.

Wong, A. L. and A. M. Haith (2017). "Motor planning flexibly optimizes performance under uncertainty about task goals." Nature communications 8(1): 1-10.

Wong, A. L., A. M. Haith and J. W. Krakauer (2015). "Motor planning." The Neuroscientist 21(4): 385-398.

Woody, E. and H. Szechtman (2002). "The Sensation of Making Sense." Psyche 8: 20.

Wu, Y.-H. and M. L. Latash (2014). "The effects of practice on coordination." Exercise and sport sciences reviews 42(1): 37.

Wu, Y.-H., N. Pazin, V. M. Zatsiorsky and M. L. Latash (2013). "Improving finger coordination in young and elderly persons." Experimental brain research 226(2): 273-283.

Xia, X., D. Wang, Y. Song, M. Zhu, Y. Li, R. Chen and J. Zhang (2020). "Involvement of the primary motor cortex in the early processing stage of the affective stimulus-response compatibility effect in a manikin task." NeuroImage 225: 117485.

Xie, X., N. Fan and N. Wang (2019). Retrograde Transneuronal Injury: From the Posterior Optic Pathway to Retinal Ganglion Cells. Optic Disorders and Visual Field, Springer: 559-572.

Yamagata, M., M. Popow and M. L. Latash (2019). "Beyond rambling and trembling: effects of visual feedback on slow postural drift."

Experimental brain research 237(3): 865–871.

Yang, L., H. Leung, M. Plank, J. Snider and H. Poizner (2014). "EEG activity during movement planning encodes upcoming peak speed and acceleration and improves the accuracy in predicting hand kinematics." IEEE journal of biomedical and health informatics 19(1): 22–28.

Ye, T., J. Peng, B. Nie, J. Gao, J. Liu, Y. Li, G. Wang, X. Ma, K. Li and B. Shan (2012). "Altered functional connectivity of the dorsolateral prefrontal cortex in first–episode patients with major depressive disorder." European journal of radiology 81(12): 4035–4040.

Zagha, E., A. E. Casale, R. N. Sachdev, M. J. McGinley and D. A. McCormick (2013). "Motor cortex feedback influences sensory processing by modulating network state." Neuron 79(3): 567–578.

Zatsiorsky, V. M. and M. L. Latash (2008). "Multifinger prehension: An overview." Journal of Motor Behavior 40(5): 446–475.

Zatsiorsky, V. M., Z.–M. Li and M. L. Latash (2000). "Enslaving effects in multi–finger force production." Experimental brain research 131(2): 187–195.

Zhang, W., J. P. Scholz, V. M. Zatsiorsky and M. L. Latash (2008). "What do synergies do? Effects of secondary constraints on multidigit synergies in accurate force–production tasks." Journal of neurophysiology 99(2): 500–513.

Zhang, W., V. M. Zatsiorsky and M. L. Latash (2007). "Finger synergies during multi–finger cyclic production of moment of force." Experimental brain research 177(2): 243–254.

Zhou, T., Y.–H. Wu, A. Bartsch, C. Cuadra, V. M. Zatsiorsky and M. L. Latash (2013). "Anticipatory synergy adjustments: preparing a quick action in an unknown direction." Experimental brain research 226(4): 565–573.

초 록

다중손가락 과제 수행 시 인간의 감각 및 인지 처리 과정의 정량화

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시시각각으로 변화하는 신체 상태와 주변 환경의 상호작용 속에서 알맞은 움직임을 수행하기 위해서는 그에 따른 즉각적인 운동 적응(motor adaptation) 과정와 과제 목표에 대한 이해가 필요하다. 이를 위해 인간의 감각 및 인지 처리과정은 운동 제어 분야의 중요한 요소로 여겨졌다. 선행연구에 따르면, 운동 과제에 따라 변화하는 감각 및 인지 처리과정은 주변 환경과 과제의 목표에 따라 움직임의 특성에 영향을 미친다고 보고되어왔다. 그러나 이러한 영향은 대부분 단순한 운동과제 수행 결과 또는 측정된 신경 활동에 의해 경험적으로 요약된 결과에 국한되어 있다. 따라서 본 논문은 다양한 움직임 특성을 가진 다중 손가락 과제 수행 시, 뇌 활동 (Brain activity)과 더불어 손가락들 간의 협응적인 움직임의 수행 결과를 동시 측정하여 과제의 특성에 따른 감각 및 인지 처리과정의 변화를 분석했다. 다중 손가락 과제는 운동 제어의 성능 효율성을 정량화하기 위해 사용되는 대표적인 과제다.

본 논문에서는 다양한 조건의 움직임 방향, 움직임의 주기빈도, 감각 피드백 양식 또는 과제 난이도에 따른 다중 손가락 회전 동작 및 힘 생성 과제를 사용했다. 연구 결과로는, (문단 3) 움직임 방향이 변화하기 전에 변화할 방향에 상관없이 협응적인 움직임이 악화되었다. (문단

4와 5) 움직임의 주기빈도가 증가할수록 협응적인 움직임이 악화됐으며, 이와 관련된 감각 및 인지 처리과정의 효율성도 감소되었다. (문단 6) 단일 감각 피드백 제공조건에 비해 종합적인 감각 피드백은 증가된 감각 처리과정과 함께 협응적인 움직임을 향상시켰다. (문단 7) 과제의 난이도가 증가할수록 협응적인 움직임과 인지 처리과정의 효율성은 감소되었으며, 움직임의 주기빈도 조건에 비해 과제의 난이도에 따라 협응적인 움직임과 인지 처리과정에 미치는 영향은 상대적으로 더 크게 나타났다. 이러한 결과는 움직임 특성에 따른 뇌 활동과 협응적인 과제 수해 결과를 통해 운동 제어 과정에서 감각 및 인지 처리과정의 기여정도를 정량화할 수 있다는 점을 시사한다. 따라서 움직임 특성에 따른 감각 및 인지 처리 과정의 기여정도의 변화는 운동 기능 장애를 가진 사람들의 새로운 재활 훈련 프로그램 및 움직임 보조 장치를 개발하기 위한 실험적인 근거로 적용될 수 있다. 또한 감각 또는 인지 과정이 운동 제어에 미치는 영향을 추정하기 위한 효율적인 방법을 개발하는데 도움이 될 것이다.

주요어 : 감각 처리과정; 인지 처리과정; 다중손가락 과제; 움직임 특성
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