

早稲田大学審査学位論文

博士（スポーツ科学）

Structure of Motor Programming:
Inference from Event-related Potentials

運動プログラミングの構造
—事象関連電位による検討—

2015年1月

早稲田大学大学院 スポーツ科学研究科

徐 璐

XU, Lu

研究指導教員： 正木 宏明 教授

PREFACE

Some of the findings presented in this thesis have been published as follows:

1. Xu, L., Sommer, W., & Masaki, H. (2015). The structure of motor programming: Evidence from reaction times and lateralized readiness potentials, *Psychophysiology*, *52*, 149-155. doi: 10.1111/psyp.12296
2. Xu, L., Sommer, W., & Masaki, H. (2014). On the structure of motor programming: An Additive Factors approach. *Sport Science Research*, *11*, 250-264.

CONTENTS

	Page
PREFACE.....	i
CONTENTS.....	ii
LIST OF TABLES.....	vi
LIST OF FIGURES.....	vii
LIST OF ABBREVIATIONS.....	ix
CHAPTER 1 INTRODUCTION.....	1
1.1 Motor Programming.....	1
1.1.1 Development of the Concept of Motor Program.....	1
1.1.2 Evidence Supporting Motor Program.....	2
1.2.3 Models of Motor Programming.....	4
1.2 Event-related potential (ERP).....	13
1.2.1 Contingent Negative Variation (CNV).....	14
1.2.2 P3.....	14
1.2.3 Readiness Potential (RP).....	15
1.2.4 Lateralized Readiness Potential (LRP).....	15
1.3 Motor Related Parameters.....	17
1.3.1 Hand Placement.....	17
1.3.2 Response Sequences.....	20

1.3.3 Movement Duration.....	21
1.3.4 Force Parameter	21
1.4 Summary	24
CHAPTER 2 ON THE STRUCTURE OF MOTOR PROGRAMMING: AN ADDITIVE FACTORS	
APPROACH	26
2.1 Experiment 1: Effects of Movement Duration and Hand Placement on Reaction Times ...	26
2.1.1 Purpose	26
2.1.2 Hypothesis.....	26
2.1.3 Methods	27
2.1.4 Results	30
2.1.5 Discussion.....	31
2. 2 Experiment 2: Effects of Movement Duration and Response Sequence Complexity on	
Reaction Times (1)	32
2.2.1 Purpose	32
2.2.2 Hypothesis.....	33
2.2.3 Methods	33
2.2.4 Results	34
2.2.5 Discussion.....	35
2. 3 Experiment 3: Effects of Movement Duration and Response Sequence Complexity on	
Reaction Times (2)	35
2.3.1 Purpose	35

2.3.2 Hypothesis.....	36
2.3.3 Methods	36
2.3.4 Results.....	37
2.3.5 Discussion.....	38
2.4 Summary	38
CHAPTER 3 FUNCTIONAL LOCI OF MOTOR PARAMETERS: EVIDENCE FROM	
REACTION TIMES AND LATERALIZED READINESS POTENTIALS	39
3.1 Experiment 4: Motor Programming of Hand Placement and Response Sequence Length .	39
3.1.1 Purpose	39
3.1.2 Hypothesis.....	39
3.1.3 Method	40
3.1.4 Results.....	43
3.1.5 Discussion.....	46
3.2 Experiment 5: Motor Programming of Movement Duration and Response Sequence	
Complexity.....	46
3.2.1 Purpose	46
3.2.2 Hypothesis.....	47
3.2.3 Method	47
3.2.4 Results.....	51
3.2.5 Discussion.....	54
3.3 Summary	54

CHAPTER 4 NEURAL CORRELATES OF MOTOR PARAMETER SPECIFICATION: EVIDENCE FROM CONTINGENT NEGATIVE VARIATIONS	56
4.1 Experiment 6: Effect of Force Parameter Modification on the Contingent Negative Variation	56
4.1.1 Purpose	56
4.1.2 Hypothesis.....	56
4.1.3 Method	57
4.1.4 Results	62
4.1.5 Discussion	69
4.2 Summary	69
CHAPTER 5 GENERAL DISCUSSION	70
5.1 Organization Structures of Motor Programming	72
5.2 Functional loci of Effects of Motor Parameters	77
5.3 Central Representations of Motor Parameter Specifications	83
5.4 Conclusion	87
5.5 Limitation and Perspectives	88
REFERENCES	91

LIST OF TABLES

Table	Page
3-1 Mean RT (ms), error rate (%), mean P3 intervals (ms), and mean LRP intervals (ms)	43
3-2 Mean RT (ms), error rate (%), and mean LRP intervals (ms).....	52

LIST OF FIGURES

Figure	Page
Figure 1-1 Additive factor method logic.....	6
Figure 1-2 Stage structure of traditional choice reactions.....	8
Figure 1-3 HED model and two-process model in choice RT tasks.....	11
Figure 1-4 Cascade model.....	12
Figure 1-5 Stimulus-locked and response-locked LRPs.....	16
Figure 1-6 Un-crossed and crossed hands.....	18
Figure 2-1 Hypothesized structure of motor programming.....	27
Figure 2-2 Effect of factors hand placement, sequence complexity, and movement duration on mean RTs.....	30
Figure 2-3 Effect of factors hand placement, sequence complexity, and movement duration on mean error rates.....	31
Figure 3-1 Grand averaged waveforms of P3.....	44
Figure 3-2 Grand averaged waveforms of LRPs.....	45
Figure 3-3 Grand averaged waveforms of LRPs.....	53
Figure 4-1 Procedure of precue paradigm adopted in the force production task.....	58
Figure 4-2 Match of 10 N trials between the single- and multiple-target tasks.....	60
Figure 4-3 RTs in the single- and multiple-target tasks.....	62
Figure 4-4 Exerted force in the single- and multiple-target tasks.....	63
Figure 4-5 Time to peak force in the single- and multiple-target tasks.....	64

Figure 4-6	CNVs waveforms averaged from 10 N trials in the single- and multiple-target tasks.....	65
Figure 4-7	Difference waveforms and topographies calculated by subtracting the CNVs in the single-target task from the multiple-target task.	67
Figure 4-8	Foreperiod LRPs waveforms averaged from 10 N trials in the single- and multiple-target tasks.....	68

LIST OF ABBREVIATIONS

AFM	additive factor method
ANOVA	analysis of variance
BP	Bereitschaftspotential
CNV	contingent negative variation
EEG	electroencephalogram
EMG	electromyogram
EOG	electrooculogram
ERP	event-related potential
HED	hierarchical editor
Hz	Hertz
LRP	lateralized readiness potential
LRP-R	response-locked LRP
M	mean
ms	millisecond
μV	microvolt
R	response
RP	readiness potential
RT	reaction time
s	second
S	stimulus
S-LRP	stimulus-locked LRP
SRC	stimulus-response compatibility
TTP	time-to-peak force

CHAPTER 1 INTRODUCTION

1.1 Motor Programming

To produce actions, our brain sends appropriate motor commands to synchronize the contractions and relaxations of relevant muscles. These commands consist of both spatial and temporal parameters necessary for movement execution, including speed, duration, force, direction, and effector (Sanders, 1998; Verwey, 1994; Zelaznik & Franz, 1990). The specification of such motor commands is widely believed to be controlled by a central motor program (for reviews see Keele, 1981; Rosenbaum, 1985), which is the main topic of the present study.

1.1.1 Development of the Concept of Motor Program

As a term borrowed from computer science, motor program was firstly regarded as sets of muscle instructions (Keele and Summers 1976). The most common concept of motor program comes from Keele (1968). He defined it as “a set of muscle commands that are structured before a movement sequence begins, and that allows the entire sequence to be carried out uninfluenced by peripheral feedback” (p.387). Several years later, in a review of recent motor program studies, Keele (1981) considered motor program as abstract non-muscle-specific representations of motor acts (see also, van Galen & Teulings, 1983). Schmidt (1982) further developed the concept of motor program as “an

abstract memory structure prepared before the movement which, when executed, results in movement without the involvement of feedback requiring a correction for an error in selection” (p.205).

Other researchers defined the concept of motor program without specifying ballistic control of the movement. For example, Shaffer’s (1982) defined motor program as “a set of grammatical representations of intended action constructed, by a control system, as a hierarchy of abstractions, terminating in motor output” (p.110). Van Galen and Teulings (1983) simply defined the motor program as “the central representation of an ordered sequence of movement elements” (p.10).

1.1.2 Evidence Supporting Motor Program

In human information processing research over the last century, at least three separate stages or processes have been proposed to intervene between the presentation of a stimulus and the initiation of a response (e.g., Schmidt, 1988). First, in the stimulus-identification stage, the individual must detect and identify features of the stimulus present in the information processing flow. Delayed identification of the stimulus results in delayed reaction time (RT). In the second stage, response selection following stimulus identification, the individual must decide what response to make to the stimulus. The decision is often related to not only the selection of a proper response but also to ignoring the stimulus to make no response at all. Finally, in the response programming stage, the individual must organize and initiate the proper movement

selected in the response selection stage. An appropriate motor program must be assembled, prepared for activation, and executed to produce the required response in this stage. The more complex the required movement, the more time needed to assemble the proper motor program. In addition, in the case of producing a ballistic movement modulated by feedforward control, it is the motor program that is critical to actualize the movement.

The theory that the control of a rapid movement can be exclusively expressed by its motor program is supported by several lines of evidence. For instance, rapid movements are completed before feedback can be returned and processed, suggesting that feedback processing is minimally required to make a rapid movement. In addition, patterns of electromyograms (EMGs) are unaffected immediately after an unexpected mechanical block of a movement. Wadman, Denier van der Gon, Geuze, and Mol (1979) reported agonist (triceps) and antagonist (biceps) EMG activity in a rapid elbow-extension task, resulting in a distinct three-burst EMG pattern; (a) a burst of the agonist muscle, (b) a burst of the antagonist muscle preceded by turning off of the first agonist activity, and (c) the second agonist burst near the end of the movement. They found similar EMG patterns for about 110 ms after the first agonist EMG burst, even when they recorded the EMG patterns in the mechanically blocked trials in which the lever to be moved was unexpectedly locked at the starting position on some trials, suggesting that the movement was prestructured. These facts support the notion that central programming

controls rapid movement. In addition, Henry and Rogers (1960) corroborated that RTs increase with response complexity, resulting in longer movement duration in itself, even though RT is a measure of the interval between the stimulus and the response onset. This finding also supports the hypothesis that rapid movements are structured in advance and that the response programming stage needs more time to plan the complex movement.

Furthermore, deafferentation studies have shown that a rapid movement can be produced without feedback, although exhaustive control of movements is degraded. Kelso (1977) studied accuracy in a blind finger-positioning task in which participants defined (preselected) their own movements and were deprived of proprioceptive feedback from joint and cutaneous sources through use of a nerve block applied to the wrist in deprived feedback condition. No significant differences in error were found between normal and deprived feedback conditions, indicating that preselected movements were not dependent on peripheral cues gaining access to central awareness. This finding suggests that feedback information is not critical for a movement to occur. All these findings strongly support a view that motor programs control a ballistic movement.

1.2.3 Models of Motor Programming

One important goal in mental chronometry research is to reveal the organization structure of motor program. In other words, to investigate how various motor

parameters are structured by central motor programming processes. Specifically, whether this takes place within a unitary stage or within different separable motor processes and how these processes are organized. There are several models accounting the stage structure of motor programming to be reviewed.

1.1.2.1 Stage Structure of Choice Reactions

Additive Factor Method

A first account relies on the *additive factor method* (AFM) proposed by Sternberg (1969). The basic assumption of the AFM is that information processing proceeds through a set of sequentially ordered and independent stages; the total RT is the sum of time demands for each stage. To determine the presence of independent processing stages using the AFM logic, two or more experimental factors are orthogonally manipulated; each factor varies across two or more levels of difficulty affecting the time demands of processing and hence RT. If the factors manipulated affect at least one common stage, one should observe interactions (Figure 1-1).

An *overadditive* interaction occurs when a factor has a greater effect on the more time demanding level of the other factor, whereas an *underadditive* interaction occurs when a factor has a greater effect on the less time demanding level of the other factor (Stanovich & Pachella, 1977). An overadditive interaction indicates that at least one common stage is affected by the manipulated factors, whereas an underadditive

interaction suggests parallel or overlapped processes within stages. If the experimental factors affect independent stages, only *additivity* without interaction should be observed.

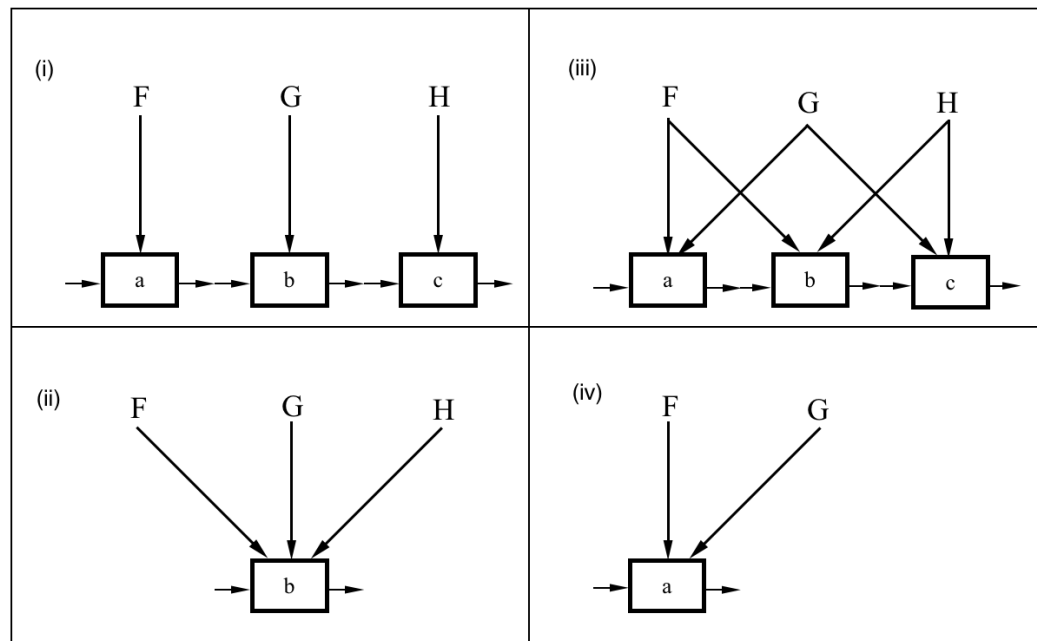


Figure 1-1. Additive factor method logic (Adapted from Sternberg, 1969). Pannel (i): Additive effects of variables (F, G, H); Pannel (ii, iii, iv): Interactions suggest at least one common stage.

Stage Structure of Choice Reactions

Based on additive and interactive effects reported in the literature, Sanders (1990) proposed that a stage structure for processing choice response tasks as follows: Stimulus preprocessing, feature extraction, identification, followed by response selection, motor programming, and motor adjustment (Figure 1-2, reviewed in Sanders, 1998).

The first motor-related stage is called *response selection* based on the additive effects of stimulus quality and stimulus response compatibility (SRC). During this stage, perceptual codes are translated to abstract response codes. SRC was first reported by Fitts (Fitts & Deininger, 1954; Fitts & Seeger, 1953), refers to the observation that some tasks are easier to perform than others when either (1) the particular sets of stimuli and responses are used, or (2) individual stimuli and responses are paired (Kornblum, Hasbroucq, & Osman, 1990). For example, in so-called symbolic SRC, stimuli (letters or words) signifying “left” or “right” are paired with responses on the side indicated by the stimulus (compatible) or on the other side (incompatible). Number of response alternatives, precueing, and relative S-R frequency were also shown to influence this stage (Sanders, 1998).

According to an observed interaction between instructed speed and movement direction, Spijkers (1987) concluded that response selection is followed by a *motor programming* stage. Kinematic parameters of the response code are specified and established during motor programming. It is noteworthy that an orthogonal manipulation of SRC that is thought to influence the response selection and “crossed hands” revealed additive effects, suggesting that crossed hands influence motor-programming but not response selection (Sanders, 1998; see also Leuthold & Sommer, 1998). The factor of crossed hands (also named hand placement) is manipulated in performing two-choice key-presses with hands (or other limbs) placed

either in normal or crossed over position (Kornblum, et. al, 1990). RT becomes slower when hands are crossed (e.g. Riggio, Gawryszewski, & Umilta, 1986; Matsumoto, Misaki, & Miyauchi, 2004).

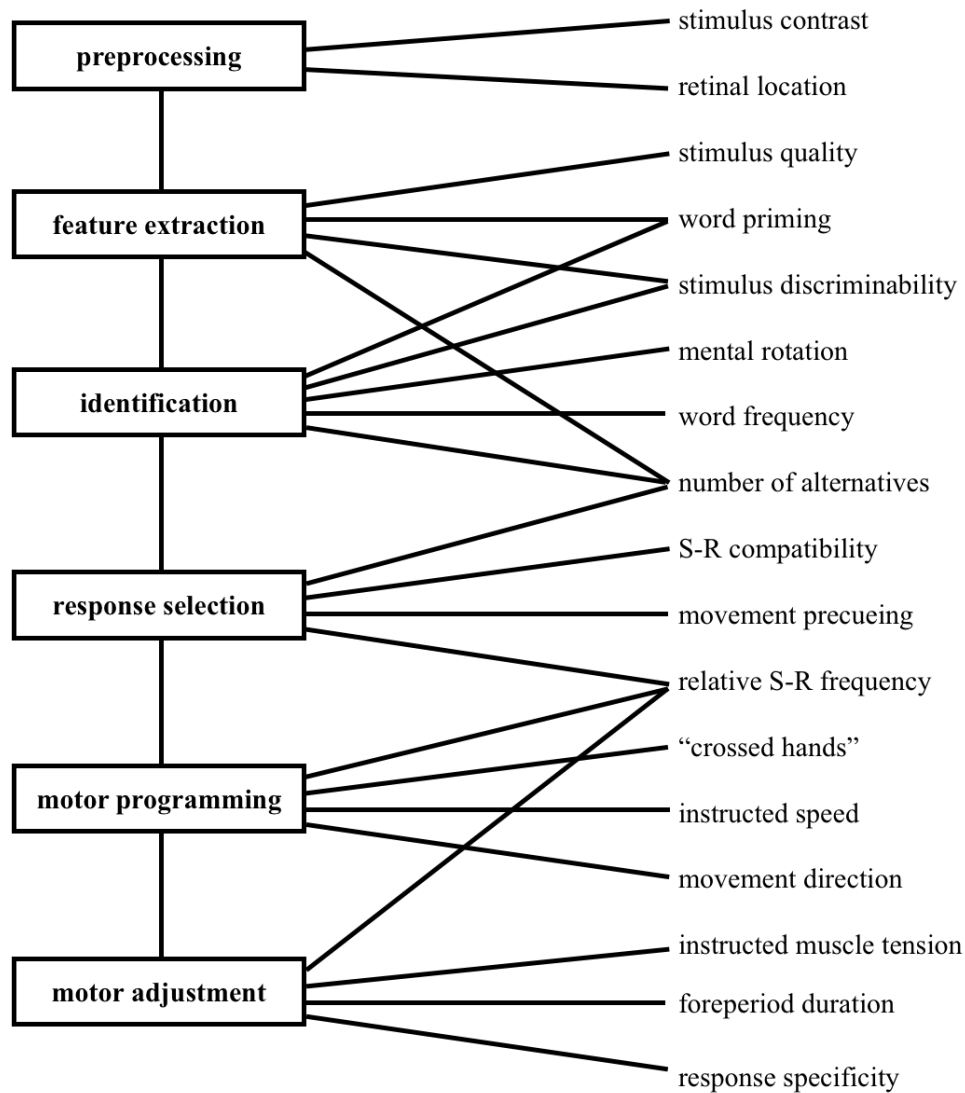


Figure 1-2. Stage structure of traditional choice Reactions (adapted from Sanders, 1998)

Left side shows stages during information processing; right side shows factors which might affect one or more stages.

The *motor adjustment* stage that is thought to follow the motor-programming stage deals with the transition from central to peripheral motor activity. Previous studies showed that the motor adjustment stage is affected by foreperiod duration, instructed muscle tension, and response specificity (Sanders, 1998). Spijkers and Steyvers (1984) found additive effects of foreperiod duration and movement duration. If the foreperiod duration effects were localized in the motor adjustment stage, it is highly possible that movement duration affects another motor-related stage. So far movement duration has been tested in a sliding movement task (Spijkers & Steyvers, 1984) and a key pressing task (Zelaznik & Hahn, 1985). RTs increased for the longer movement durations in both tasks.

1.1.2.2 Generalized Motor Programs

Schmidt (1975) expanded the motor program notion to a more generalized one, pointing out that the early motor program view includes two problems: those of storage and novelty. The *storage problem* relates to the idea that the number of programs that express various movements is so large that their storage in the central nervous system seems inefficient and even impossible. The *novelty problem* relates to the issue that the original motor program theory cannot explain the fact that the participant can produce a novel movement that has not been produced before. To solve these concerns, Schmidt (1975) proposed a notion of the *generalized motor program* (GMP). It is a motor program stored in memory as an abstract form of function for a particular class of

movement, which can be adapted to a unique pattern of movement by supplying a certain parameter to it. Hence, certain parameters must be applied to the generalized motor program to specify how the movement is to be expressed. In other words, the expression of the motor program can be varied depending on the choice of the parameters. Such parameters include the overall duration of the movement, which defines the overall duration of the program's action, overall force of the contractions with which the recruited muscles will contract, and the selection of the muscles or limbs to be used in the movement (Schmidt, 1988). It should be noted that some studies (Shea & Wulf, 2005; Leuthold & Jentsch, 2011 among many others) regarded relative force as a GMP, however, Schmidt (Schmidt, 2003) has pointed out that relative force is not invariant. The relative force is a parameter that scales muscles.

1.1.2.3 Other Models Accounting for Motor Programming

Hierarchical Editor (HED) Model

A third and more elaborate account of the motor programming phase was proposed by Rosenbaum and colleagues (Rosenbaum, Inhoff, & Gordon, 1984; Rosenbaum, Hindorff, & Munro, 1987). They introduced a hierarchical organization of motor programming. According to the *hierarchical editor (HED) model*, two processes occur successively to produce a movement sequence. The first process is named *edit pass*, during which the unspecified responses are unpacked from a representation in long-term

memory and then specified into smaller response elements. This unpacking process proceeds hierarchically, from higher level to lower nodes. When the motor programs cannot be decomposed anymore, the *execution pass* occurs to execute each specified element in turn (Figure 1-3).

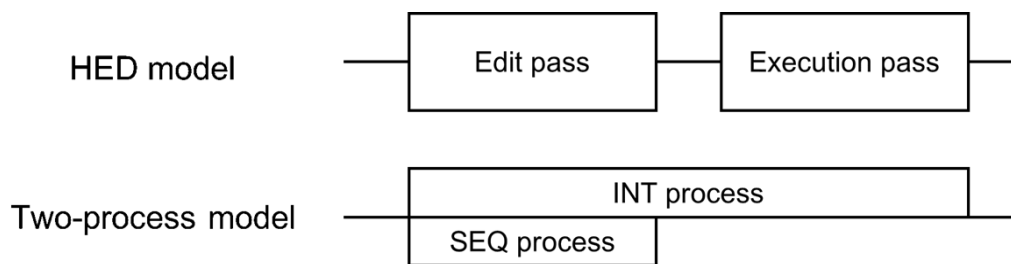


Figure 1-3. Hierarchical editor (HED) model and two-process model in choice RT tasks

Two-process Model

Another account is Klapp's two-process model (Klapp, 1995; 2003). The two-process model proposes that motor programming is controlled by two processes concerning the internal features (the *INT* process) and sequences (the *SEQ* process) of movement elements, respectively. It is assumed that the two processes occur serially in simple RT and in parallel during choice RT tasks. Moreover, the *INT* process, which is more time consuming than the *SEQ* process, can be preprogrammed in simple RT but not in choice RT. Thus, one difference between the HED and Klapp's model is that the former assumes movement parameters are organized serially rather than in parallel in choice RT tasks (Figure 1-3).

Cascade Model

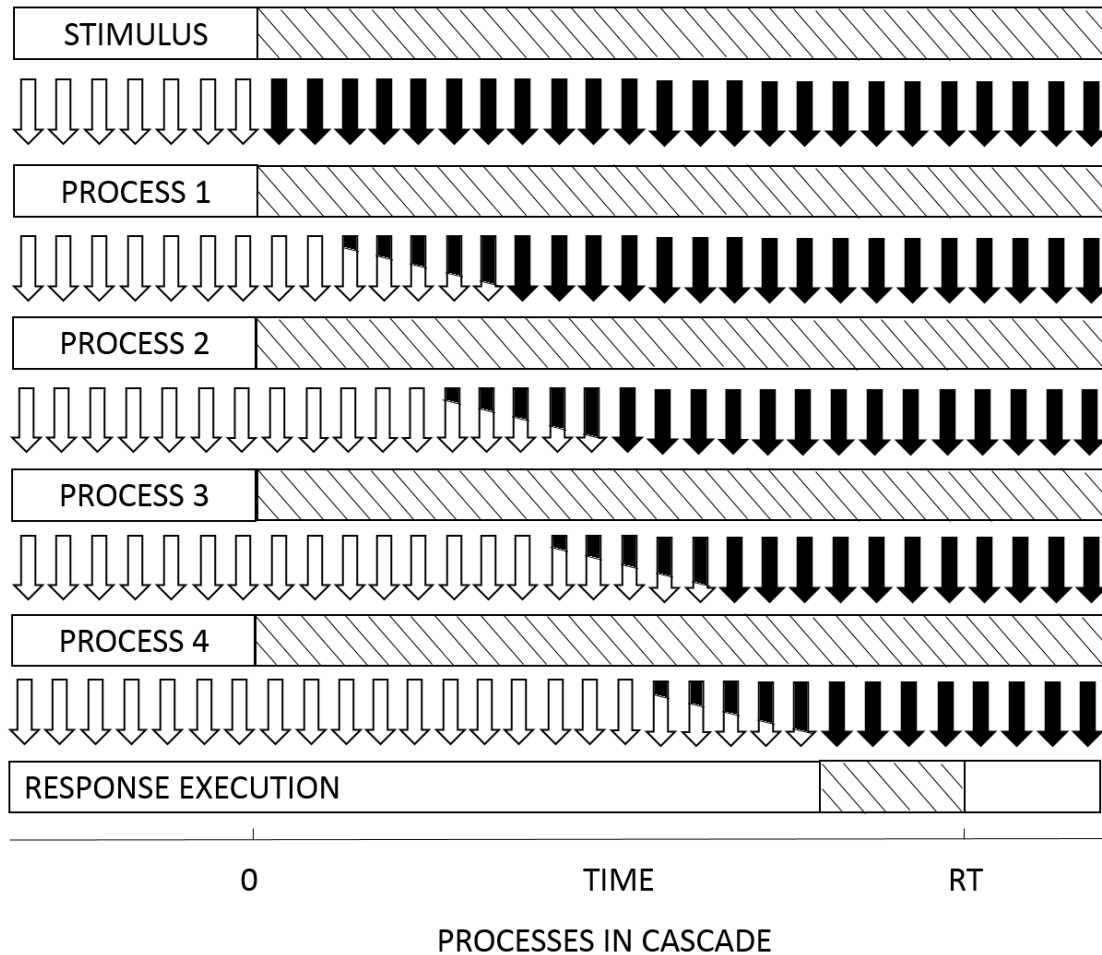


Figure 1-4. Cascade model (adapted from McClelland, 1979)

Cascade model is a typical continuous model proposed by McClelland (McClelland, 1979) based on mathematical modeling (Figure 1-4). As other models, the cascade model has its own postulates: firstly, it assumes a unidirectional information flow among continuously activated but functional independent *subprocesses*, or named *processing levels*. On contrary to the discrete stage models, these subprocesses can be active simultaneously in parallel, and the output of each subprocess is always available

for the next processing level. In the end, if reached threshold of the so-called *response activation process*, one of the possible alternative responses will be executed by adding a discrete stage between the stimulus processing and the emitting of the overt response. Another important assumption of the cascade model is that each subprocess consists of numbers of processing units. These units accumulate information at a certain *rate* until reaching an *asymptotic activation level*. The activation rate of a unit depends on the difference between levels. Based on the simulations of factorial manipulations of parameters, McClelland proposed two possible explanations for the additive effects: either the rates of different processes are affected, or one affects the rate of a fast process and another affects the asymptotic activation level. On the other hand, the AFM logic explains the additive effects of two factors as that they affect at least two separate and independent stages.

1.2 Event-related potential (ERP)

Behavioral studies based on the AFM logic can provide information concerning the end product of processing and whether or not experimental factors interact. However, they are not informative about the ordering of separable stages. Generally, to interpret the underlying mechanisms of behavioral effects represented in RTs, event-related potentials (ERPs) are helpful (Coles & Rugg, 1995). ERPs are extracted from the electroencephalogram (EEG) usually by averaging and consist of distinct components with functional specificity, allowing tracking psychologically meaningful processes at

high temporal resolution.

Until now ERPs have been used as a powerful tool and extensively used in studies of human information processing to clarify the processes underlying various human behaviors. Here review several movement-related ERP components, which can serve as useful tools for investigating movement preparation.

1.2.1 Contingent Negative Variation (CNV)

The contingent negative variation (CNV) (Walter, Cooper, Aldridge, McCallum, & Winter, 1964) is a slow negative-going wave. It is usually observed in paradigms where a warning stimulus (S1) is followed by an imperative stimulus (S2) requiring a response. Järviletho and Frühstorfer (1970) first reported a frontally-distributed early component associated with orienting response to S1 and a centrally-distributed late component associated with response preparation (see also, Loveless & Sanford, 1974). Later studies have reported larger late CNVs for stronger force exertions (Low & McSherry, 1968), more rapid force increments (van Boxtel, van den Boogaart & Brunia, 1993), and faster responses with emphasis on response speed (e.g., Rohrbaugh, Syndulko, & Lindsley, 1976), suggesting relationships between the late CNV and some motor aspects.

1.2.2 P3

P3 is a positive ERP component peaking at about 300 ms after stimulus onset with a central-parietal distribution. The latency of P3 is defined as the time interval between

stimulus onset and the time point of maximal positive amplitude within certain time window. The P3 latency is considered to represent stimulus evaluation and sensitive to both stimulus- and response-related factors (Ilan & Polich, 1999; Verleger, 1997). However, some studies showed that P3 is independent of response selection (Kutas, McCarthy, & Donchin, 1977; Leuthold & Sommer, 1998; Magliero, Bashore, Coles, & Donchin, 1984).

1.2.3 Readiness Potential (RP)

Another slow wave in the ERP, preceding a self-paced movement, is referred to as readiness potential (RP) (Vaughn, Costa, & Ritter, 1968). It emerges up to 2 s prior to a voluntary movement. It includes a gradual negativity, Bereitschaftspotential (BP) (Kornhuber, & Deecke, 1965), and a steeper negative slope (NS'). The RP is considered to be included, at least partly, in the late CNV, and the distribution of the later CNV is more complex than the RP (for details, see Brunia, 2003).

1.2.4 Lateralized Readiness Potential (LRP)

From the RP a useful ERP component can be extracted, the so-called lateralized readiness potential (LRP). It is obtained by subtracting the RP recorded over electrode sites ipsilateral to the responding hand from the RP recorded over contralateral sites. The LRP is considered to represent the activation of effector-specific response-related processes (Coles, 1989; Miller, Riehle, & Requin, 1992). Thus, as soon as the LRP

deviates from zero into a negative voltage direction, the response hand, required for the task is activated. More specifically, it has been shown that the LRP starts after response hand selection with the beginning of motor programming (Masaki, Wild-Wall, Sangals, & Sommer, 2004).

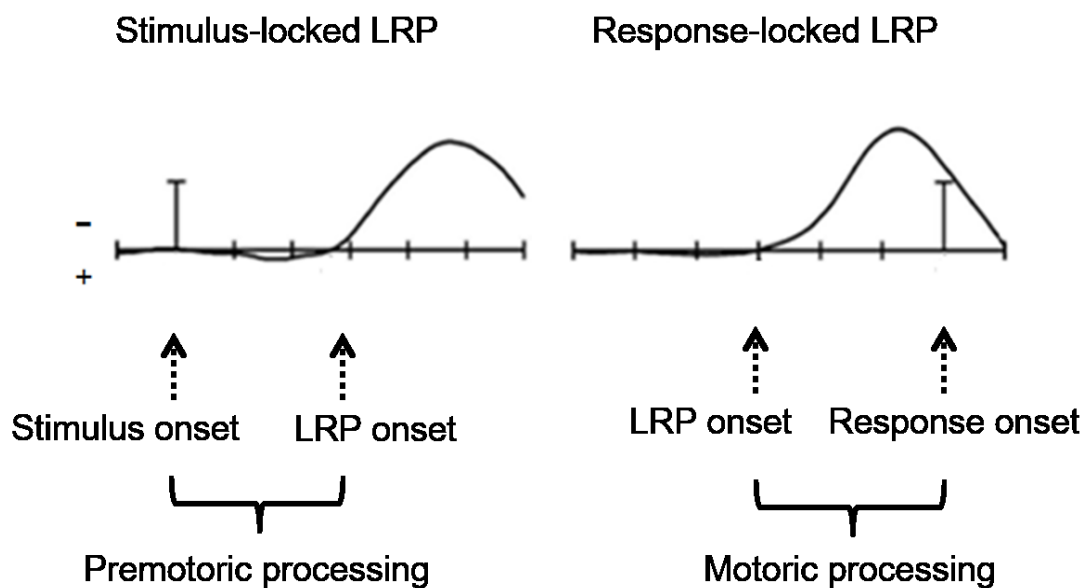


Figure 1-5. Stimulus-locked and response-locked LRPs

Thus, the interval between the onsets of the imperative stimulus and the stimulus-locked LRP (i.e., S-LRP interval) is considered to represent the duration of processes preceding hand-specific preparation (i.e., perceptual processing and response selection); the interval from the onsets of the response-locked LRP to the overt response (i.e., LRP-R interval) is used to infer the duration of response-related processes (Schröter & Leuthold, 2009) (Figure 1-5). The LRP-R interval has been shown to be sensitive to the precuing of fingers (Osman, Moore, & Ulrich, 1995), time-to-peak (TTP)

force (Masaki et al., 2004) and of movement direction (Müller-Gethmann, Rinckenauer, Stahl, & Ulrich, 2000; Leuthold, Sommer, & Ulrich, 1996), and to response complexity (Low, Miller, & Vierck, 2002; Smulders, Kok, Kenemans, & Bashore, 1995). Thus, if we observe experimental effects on the S-LRP interval, we may conclude that the factor producing the effect influences processes preceding hand-specific preparation. If we observe effects on the LRP-R interval, we may conclude that the factor affects motoric processes.

1.3 Motor Related Parameters

In the following paragraphs I will briefly review previous reports about experimental factors which might affect motor-related stages.

1.3.1 Hand Placement

Previous research reported increased choice RTs when response hands were placed cross-wise as compared to normal positions (i.e., Kornblum, et al., 1990). This prolongation of RTs is referred to as *crossed-hand effect* (Matsumoto, et al., 2004; Riggio, et al., 1986) or *hand placement effect* (Leuthold & Sommer, 1998) (Figure 1-6). The effects of hand placement have been found for both visual stimuli (Brebner, et al., 1972; Brebner, 1973; Klapp, Greim, Mendicino, & Koenig, 1979; Nicoletti, Umiltà, & Ladavas, 1984; Wallace, 1971, 1972) and auditory stimuli (Callan, Klisz, & Parsons, 1974; Simon, et al., 1970).

Many efforts have been made to reveal the underlying mechanism of hand placement effects in behavioral studies. For example, Simon et al. (1970) confirmed the importance of compatibility between stimulus and response locations in auditory modality. In the visual modality, Nicoletti et al. (1984) attributed the hand placement effect to the relative position of responding hands, rather than to the unnatural posture or the relative position to the sides of the body.

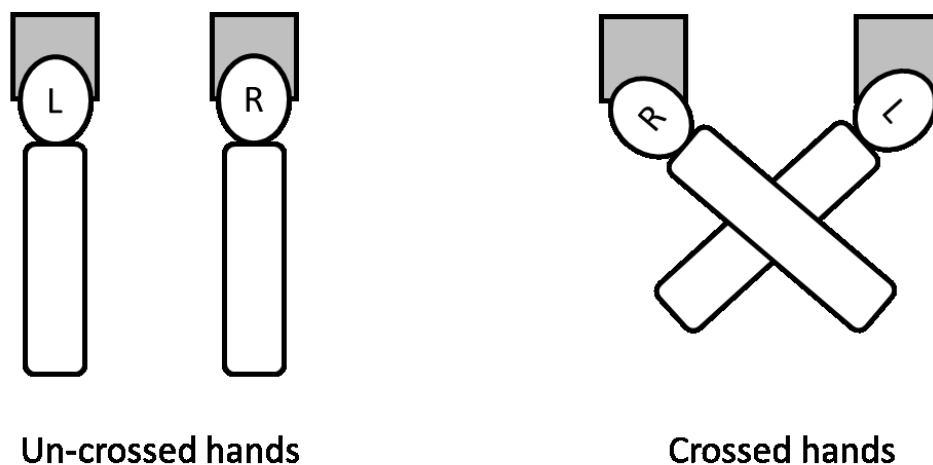


Figure 1-6. Un-crossed and crossed hands

Riggio et al (1986) investigated the crossed-effector effect in choice RT tasks. In their first experiment, responses were given with index fingers, which were either uncrossed or crossed, whereas the hands were always in uncrossed position. Thus, both S-R compatibility and effector position were manipulated. In the second experiment, participants performed the choice RT task with a stick held in each hand. In this situation, the sticks were either crossed or uncrossed instead of the effectors, thus a spatial conflict between stimuli and response goals (i.e., response keys) was

manipulated. The main findings of the two experiments showed a lengthening of RT when stimuli and response goals were conflicting even with uncrossed hands. These results suggest that the effects of crossing hands are due to a mismatch between the responding hand and the locus of the response goal.

Although neural mechanisms of hand placement effects were less frequently investigated, an fMRI study reported activation of the superior temporal sulcus associated with response selection in a crossed-hand position (Matsumoto et al., 2004).

Evidences from both behavioral and psychophysiological studies suggest possible functional loci of hand placement effects. In chronometric studies, additive effects of stimulus-response compatibility (S-R compatibility) and hand placement were found with both visual stimuli (Brebner et al, 1972; Wallace, 1971) and auditory stimuli (Simon et al., 1970). Because the effect of S-R compatibility has been associated with response selection (for reviews, see Sanders, 1998), hand placement may affect either earlier (e.g. perceptual) or later (i.e., motoric) processes than response selection. Previous ERP studies did not find effects of hand placement on P3 latency (Leuthold & Sommer, 1998; Ragot, 1984), suggesting that stimulus evaluation or earlier processes are not responsible for the hand placement effect.

Nevertheless, no direct evidence was collected to support such assumption. Thus little is known about the functional locus of the hand placement effect in choice RT tasks. Specifically, it remains unclear which mental sub-process is affected by the hand

placement.

1.3.2 Response Sequences

Henry and Rogers (1960) first reported the response complexity effect on RT, while increasing complexity across three tasks. They found that RT (measured from stimulus to response onset) was 20% longer for moderately complex movements as compared to the simplest movement, and was further slowed by additional complexity. Smulders et al. (1995) investigated the effects of stimulus quality and response complexity in a choice RT task. Results suggested no effect of response complexity on the S-LRP intervals but longer LRP-R intervals were found with more complex responses. In another study adopting the AFM logic, Low et al (2002) manipulated size discriminability and response complexity in a choice RT task. They found longer LRP-R intervals in the complex conditions for both Parkinson's and control groups. In a more recent study, Leuthold and Schröter (2011) examined the programming of finger movement sequences with different complexities in a response precuing task. Participants tapped fingers either homogeneously or heterogeneously while precues provided different amounts of information. Higher structural complexity of response sequences resulted in longer RTs. They also found larger CNV amplitudes in medial motor regions in the more complex condition, and larger RP amplitudes in contralateral motor regions just before response execution, suggesting that sequence complexity influences both preparation- and execution-related activities.

1.3.3 Movement Duration

Movement duration is commonly tested in either of two tasks. One is the sliding movement task, in which participants move a stylus from a departure point to a target point and where the duration of movement is manipulated (Spijkers & Steyvers, 1984). The other task requires key presses of different durations (Klapp, Wyatt, & Lingo, 1974; Zelaznik & Hahn, 1985). In both tasks RT increases with longer movement duration. Spijkers and Steyvers (1984) combined foreperiod duration and movement duration and found additivity. It was suggested that the foreperiod duration effect was localized in the motor adjustment stage (Spijkers, 1987; Sanders, 1980). However, based on LRP findings Müller-Gethmann and her colleagues (Müller-Gethmann, Ulrich, & Rinkenauer, 2003) asserted that foreperiod manipulation affected pre-motor rather than late motoric processes. Since the locus of foreperiod effect is controversial, it is not a firm basis for drawing conclusions about a locus of movement duration effects. Compared with response complexity, movement duration has been less frequently investigated. One of the aims in this study was therefore to clarify the locus of the movement duration effect.

1.3.4 Force Parameter

Masaki, Takasawa, and Yamazaki (1997) tried to investigate the effect of force parameter modification applied to the motor program on the RP (Kornhuber & Deecke, 1965). In their study, the participant was instructed to pull a trigger in a ballistic fashion to produce a target force (1300gf: about 13.3 N) in the single-target task, and to produce

three targets (500, 1300, and 2100 gf) in the multiple-target task. The target to be produced was cued by visual stimuli every trial. They found a specifically increased negative slope (NS') of the RP (i.e., a late RP component; Shibasaki, Barrett, Halliday & Halliday, 1980) in the multiple-target task, even though the RPs were compared for the same target force trials across the two tasks. Based on Schmidt's model, a different force parameter might be applied for the invariant motor program every trial to produce the required force in the multiple-target task. Hence they concluded that the increased RP was due to a process associated with the force parameter modification.

In a further study confirming the similar effect on the RP (Masaki, Takasawa, & Yamazaki, 1998a), it was predicted that when a different target force is produced every trial (i.e., analogous to the multiple-target task of Masaki et al., 1997), it would simply induce the force parameter modification, whereas when the preceding trial is a visual tracking task governed by a different motor program, it might facilitate reassembly of the motor program to execute the target-force production task in the next trial. They found larger RPs in both motor-program reassembly task and force parameter modification task compared to the single-target task. Although the effect of the force parameter modification was confirmed by this study, the difference between the parameter modification and motor program reassembly effects on the RP remained unclear. In addition, the temporal relationship between the intention to act and applying the force parameter for the motor program was not obvious. If the augmentation of the

RP was due to the force parameter modification, a similar effect would be observed in the CNV paradigm by reason of involvement of motoric processes. Thus, the CNV paradigm seems rather suitable for investigating the effect. The present study investigated the effect of force parameter modification using the CNV paradigm in a target force production task.

The CNV paradigm has been used for the study of the movement parameterization that runs the motor program. MacKay and Bonnet (1990) used a precued choice RT task in which the warning stimulus gave the participants full information indicating both direction (i.e., elbow flexion or extension) and force (weak or strong) of the forthcoming movement, partial information indicating direction or force level only, or no information. They found that the CNV derived from the postcentral region significantly increased in the order of partial force, partial direction, and full information. Using a similar paradigm, Ulrich, Leuthold, and Sommer (1998) also found a systematical increase of the CNV associated with the amount of advance movement information given by the precue, suggesting that the CNV may reflect assembling of the motor program.

In addition, the LRP is a candidate for a useful and powerful tool for response activation in the study of human performance (e.g., Coles, 1989; Gratton, Coles, Sirevaag, Eliksen, & Donchin, 1988; Hackley & Miller, 1995). Ulrich et al (1998) investigated the assembling process of the motor program using the LRP observed in the

foreperiod. They manipulated movement parameters of response hand (right or left hand), direction (flexion or extension), and force (weak or strong). Partial precues provided information about response hand, hand plus direction, or hand plus force, whereas the full precue specified all these parameters. The foreperiod LRP was largest for full precue and was not different for the both partial precues. The precue manipulations produced shortest RT for the full precue, somewhat slower for the partial precues (hand plus direction and hand plus force), and slowest for only hand precue. Although the LRP results could not completely explain the RT results, the CNV amplitude was consistent with the RT results. They concluded that the CNV may index the assembling of the motor program and the foreperiod LRP may represent the implementation of the motor program at more peripheral levels. In addition, to reconcile their RT results with the LRP, they proposed a version of the hierarchical response preparation hypothesis that the next level unit of process after the hand node within the hierarchy cannot be activated until both force and direction of the response is available.

1.4 Summary

In sum, manipulating motor-related factors allows us to investigate the organizational structure of motor programming. No concrete conclusion about the internal structure of motor programming can be drawn from the studies reviewed on movement processing. Thus little is known about how kinematic parameters, such as movement duration or complexity, are structured by the central motor program, as well as its neural

mechanisms.

Therefore, the purpose of the present study was (1) to investigate how different motor parameters are organized during motor programming, whether it is a unitary stage with interactions between different kinds of parameters or whether each parameter is set independently of the others; (2) to confirm the functional loci of motor parameters during motoric processing; (3) to reveal the underlying neural mechanism of motor parameter specification. Six experiments were conducted to this aim.

CHAPTER 2 ON THE STRUCTURE OF MOTOR PROGRAMMING: AN ADDITIVE FACTORS APPROACH

The purpose was to reveal the organization structure of motor programming, whether it is a unitary stage, or separable consisting of subprocesses. To this aim, three experiments were conducted, manipulating different combinations of motor parameters. If motor programming is a unitary stage, the manipulated parameters should interact with each other. Otherwise, if it is separable, parameters should show additive effects without interactions.

2.1 Experiment 1: Effects of Movement Duration and Hand Placement on Reaction Times

2.1.1 Purpose

Experiment 1 was designed to investigate the effects of two motor-related factors, movement duration and hand placement, on RTs in a choice response task.

2.1.2 Hypothesis

According to predictions of the above-mentioned models including the AFM logic, the following hypotheses were proposed. First, both hand placement and movement duration were expected to affect RT, requiring more time for longer-duration conditions and hands were crossed. Second, if the motor programming stage is unitary, an

overadditive interaction of hand placement by movement duration should be observed in RTs. Otherwise, if hand placement and movement duration are programmed in parallel, as suggested in Klapp's two-process model, an underadditive effect of the two factors were expected on RTs; if hand placement and movement duration are programmed in separate modules, only additivity without any interaction of both factors were expected on RTs, which is in accordance with Rosenbaum's HED model (Figure 2-1).



Figure 2-1. Hypothesized structure of motor programming (A: unitary stage with factors interact each other; B: parallel substages dealing with each factor independently; C: independent substages in serial)

2.1.3 Methods

Participants

Eight healthy (no history of neurological or psychiatric disorders) participants (three females; mean age \pm SD: 29.1 \pm 6.6 yrs; all right-handed) were recruited from Waseda University's Faculty of Sport Sciences. Informed consent was obtained. The present

series of consecutive experiments was approved by the Waseda University Ethics Committee.

Stimuli and Responses

White single kanji characters, meaning left and right, subtending approximately $1.1 \times 1.0^\circ$ served as stimuli. They were randomly presented at the center of the display against the black background of a computer monitor placed 1 m in front of the participants. The presentation of stimuli and recording of RTs were controlled by a tachistoscope system (Iwatsu Isel Inc., IS-702).

Procedure

Every participant was tested in four blocks of 60 trials each, consisting of the factor combinations of movement duration (short vs. long press) and hand placement (crossed vs. non-crossed hands). In the non-crossed hand condition, both left and right response button boxes were placed on the table (with left box on the left side while right box on the right side relative to the midline). Participants placed their left and right hands on left and right response button boxes respectively in normal position. In the crossed-hand conditions, participants placed one forearm on the table and another arm on a wooden shelf of 11 cm height. Response button boxes were also placed either on the table or on the shelf, respectively, for each responding hand. The placement of the forearms was exchanged in the second half of the experiment. In the crossed-hand condition,

participants crossed their hands and pressed the left and right key with the right and left index finger, respectively. In the short duration condition, brisk key taps were required, whereas in the long duration condition, participants were instructed to keep the key depressed for a longer time. The order of blocks was counterbalanced across participants. Both speed and accuracy were stressed in the instruction to avoid possible speed-accuracy trade-off.

Each trial began with the presentation of a plus symbol ($0.6^\circ \times 0.6^\circ$) for 500 ms, which served as a fixation aid. It was replaced by one of the two kanji characters (i.e., 左 (left)/右 (right)), until a button was pressed. Intervals between a response and the next fixation cross onset ranged from 1900 to 2900 ms (in increments of 200 ms). The characters for left and right were presented in a pseudo-random order.

Data Analysis

Only correct response trials with RTs ranging from 100 ms to 800 ms were analyzed. RT was defined as the interval from the onset of the imperative stimulus to the onset of the first key press. The data on the RT and error rate were submitted to analyses of variance (ANOVAs) with repeated measures using as within-subjects factors, duration (short, long) and hand placement (uncrossed, crossed). Statistical significance was set at $p < .05$.

2.1.4 Results

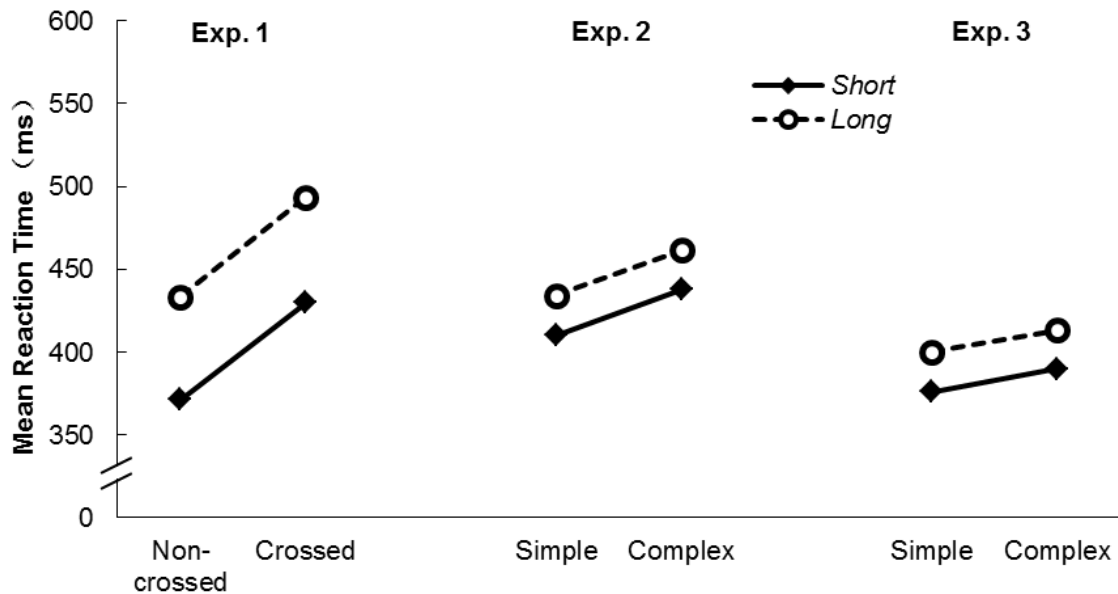


Figure 2-2. Effect of factors hand placement (experiment 1), sequence complexity (experiment 2 and 3), and movement duration on mean RTs.

Figure 2-2 (left panel) depicts mean RT. A two-way ANOVA revealed main effects of duration ($F(1,7) = 17.73, p < .01$) and hand placement ($F(1,7) = 15.10, p < .01$). RT was significantly shorter for short than long movement duration ($M = 400$ vs. 463 ms, $SEM = 15$ vs. 18 ms). RT was also longer when hands were crossed ($M = 462$ ms, $SEM = 20$ ms) than for non-crossed hand placement ($M = 402$ ms, $SEM = 14$ ms). No significant interaction was found between movement duration and hand placement ($F(1,7) = 0.02, n.s.$).

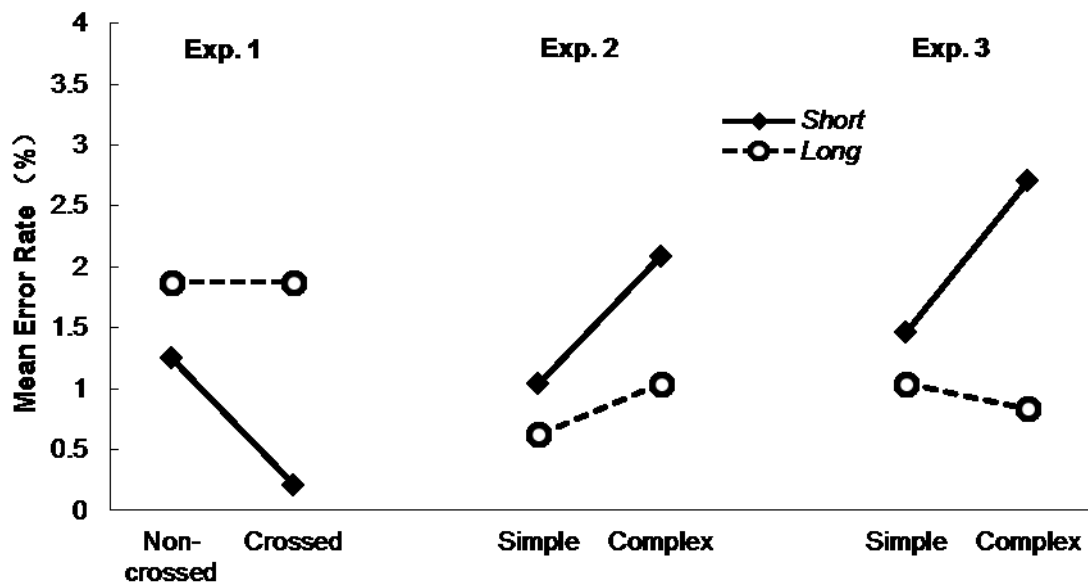


Figure 2-3. Effect of factors hand placement (experiment 1), sequence complexity (experiment 2 and 3), and movement duration on mean error rates.

Figure 2-3 (left panel) shows mean error rates. Errors occurred on less than 2% of the trials in each condition. Neither main effect of duration ($F(1,7) = 4.44, n.s.$) nor hand placement ($F(1,7) = 0.79, n.s.$) was revealed. No interaction of these factors was found ($F(1,7) = 1.84, n.s.$).

2.1.5 Discussion

In experiment 1 main effects of both duration and hand placement were found on RTs, without interaction between these factors. There was no significant effect of either factor on error rate, indicating there was no speed-accuracy trade-off in this experiment. Thus, according to the AFM logic, these results suggest that the factors movement duration and hand placement, which are both considered to influence motor

programming, do not affect a common stage. Instead, one would have to assume at least two distinct stages.

2. 2 Experiment 2: Effects of Movement Duration and Response Sequence

Complexity on Reaction Times (1)

2.2.1 Purpose

Since experiment 1 did not reveal evidence for a unitary stage of motor programming, A factor combination of movement duration with response sequence instead of hand placement was explored. The response sequence manipulation likely affects motor programming. Leuthold and Schröter (2011) tested the effect of finger movement sequences and found that more complex sequences resulted in longer RTs. A motoric locus of response sequence complexity can be suggested because this factor affected the interval between the onset of the LRP (Gratton, et al., 1988) and the response (Low, et al., 2002; Smulders, et al., 1995). If SRC does affect the response selection stage as Sanders suggested (1998), the additive effects of SRC and sequence length on choice RT reported in a previous study (Inhoff, Rosenbaum, Gordon, & Campbell, 1984) implies a motoric locus of the response sequence effect. On the other hand, Verwey (1994) suggested that the response sequence may not influence the motor-programming stage but separate sequence construction and sequence retrieval stages, preceding and following motor programming, respectively. According to Verwey (1994), the sequence construction stage is concerned with constructing a control structure or loading chunks

into a motor buffer with fixed spatio-temporal properties. Then kinematic variables, for instance, force, speed, or limb, are specified during motor programming. After that, the retrieval stage self-terminates sequential search through a non-shrinking buffer and subsequent retrieval. Both the sequence construction and retrieval stages are affected by sequence length. So far, no study has tested the combination of movement duration and response sequences of different complexity.

2.2.2 Hypothesis

According to predictions of the above-mentioned models including the AFM logic and results of experiment 1, the following hypotheses were proposed. First, both response sequence complexity and movement duration were expected to affect RT, requiring more time for more complex and longer-duration conditions. Second, if motor programming is not unitary, only main effects of both factors without interactions were expected on RTs, as shown in experiment 1.

2.2.3 Methods

Participants

Twelve healthy (no history of neurological or psychiatric disorders) participants (four females; mean age \pm SD: 27 ± 6.1 yrs; all right-handed) were recruited for this study.

Five of them participated in experiment 1.

Stimuli and Responses

Stimuli were the same as in experiment 1. Responses were recorded with three keys for each hand assigned to index, ring, and middle fingers. Participants had to either press three times with the index finger (simple sequence) or press a sequence of index, ring and middle finger (complex sequence). In addition, the first index finger press was to be either short or long according to the same criteria as in experiment 1.

Procedure

As in experiment 1, the conditions were orthogonally combined in separate blocks, counterbalanced in order across participants. There were four conditions consisting of factor combinations of movement duration (short → short → short vs. long → short → short) and sequence order (index → index → index vs. index → ring → middle). The procedure for stimulus presentation was the same as in experiment 1.

2.2.4 Results

Results are depicted in Figures 2-2 and 2-3 (middle panels). A two-way ANOVA revealed a significant main effect of response duration ($F(1,11) = 7.64, p < .05$), showing slower responses for long-duration ($M = 449$ ms, $SEM = 18$ ms) than short-duration presses ($M = 422$ ms, $SEM = 16$ ms). It also showed a significant effect of response complexity ($F(1,11) = 5.35, p < .05$). Numerically, RT was longer for complex responses ($M = 448$ ms, $SEM = 20$ ms) than simple ones ($M = 424$ ms, $SEM =$

15 ms). No interaction between these two factors was present ($F(1,11) = .001, n.s.$).

Error rate was again low ($M = 1.46\%$, range: 1.11 to 2.08%). Neither main effect of duration ($F(1,11) = 4.00, n.s.$) nor complexity ($F(1,11) = 0.62, n.s.$) was found; there was no interaction ($F(1,11) = 0.48, n.s.$). Thus no speed-accuracy trade-off occurred.

2.2.5 Discussion

In experiment 2, both the longer duration of response sequence and the more complex response sequences tended to result in longer RTs. Because there was no interaction between these factors, the data are again consistent with a non-unitary view of movement programming.

2.3 Experiment 3: Effects of Movement Duration and Response Sequence

Complexity on Reaction Times (2)

2.3.1 Purpose

To test a different response sequence in experiment 3, three-press responses were adopted with either one or two fingers (rather than three as in experiment 2). The response sequence manipulation was orthogonally combined with the duration of the third rather than the first element in the movement sequence. Keeping the first element of the movement sequence identical among conditions, allowed us to observe purer sequential effects on RTs, because effects of implementation of the first element was

eliminated.

2.3.2 Hypothesis

According to predictions of the above-mentioned models including the AFM logic and results of experiment 1 and 2, the following hypotheses were proposed. First, both response sequence complexity and movement duration were expected to affect RT, requiring more time for more complex and longer-duration conditions. Second, if motor programming is not unitary, only main effects of both factors without interactions were expected on RTs, as shown in experiment 1 and 2.

2.3.3 Methods

Participants

Eight healthy (no history of neurological or psychiatric disorders) participants (two females; mean age \pm SD: 28.6 \pm 6.9 yrs; all right-handed) were recruited for this study. Six of them participated in experiment 1. Five of them participated in experiment 2.

Stimuli and Responses

The same stimuli were presented as used in experiments 1 and 2. The factor duration, defined as in experiments 1 and 2, now concerned the duration of the third element in the response sequence and the factor sequence involved the levels of three presses with the index finger (simple) and two presses with the index followed by one press with the

ring finger.

Procedure

As before, four conditions were conducted in separate blocks. The order of conditions was counterbalanced across participants. Conditions consisted of factor combinations of movement duration (short → short → short vs. short → short → long) and sequence order (index → index → index vs. index → index → ring). In this experiment, conditions only differed in the third button press. The procedure for stimulus presentation and recording responses was the same as in experiments 1 and 2.

2.3.4 Results

Mean RTs and error rates are shown in Figure 2-2 and 2-3 (right panels), respectively. In this experiment, longer RTs – to the first element in the sequence – were found for longer key presses as the third sequence element ($M = 407$ ms, $SEM = 11$ ms) than for shorter presses ($M = 383$ ms, $SEM = 6$ ms). RTs were also longer for the complex sequence condition ($M = 402$ ms, $SEM = 9$ ms) than for the simple condition ($M = 388$ ms, $SEM = 9$ ms). A two-way ANOVA revealed main effects of both response duration ($F(1,7) = 11.83, p < .05$) and sequence complexity ($F(1,7) = 10.59, p < .05$). However, again no interaction of these factors was found ($F(1,7) = .02, n.s.$).

Mean error rate was 1.51%, ranging from 0.83% to 2.71 % across conditions. There was no experimental effect of duration ($F(1,7) = 4.44, n.s.$), or, sequence complexity

($F(1,7) = 1.84, n.s.$), nor was there an interaction of these factors ($F(1,7) = 4.81, n.s.$).

2.3.5 Discussion

Experiment 3 yielded significant main effects of both response duration and response sequence on RTs without interaction. Again, error rates were very small, and no evidence of a speed-accuracy trade-off was obtained. These findings argue against one common locus of these factors.

2.4 Summary

Three experiments were conducted to reveal the internal structure of motor programming processes. To this end three pairs of experimental factors were orthogonally manipulated. Each pair contained movement duration as a common factor, which is considered to affect the setting of parameters in the motor programming stage (Klapp & Erwin, 1976). The other factors manipulated in this study (i.e., hand placement in experiment 1, and movement sequence complexity in experiment 2 and 3) have been also related to motor programming stage (Sanders, 1998). Main effects were repeatedly obtained of all experimental factors. Importantly, there was no interaction between two factors manipulated in a given experiment. According to the AFM logic, at least two independent motor programming processes are suggested to exist, which argues against the view of motor programming being a unitary stage.

CHAPTER 3 FUNCTIONAL LOCI OF MOTOR PARAMETERS: EVIDENCE FROM REACTION TIMES AND LATERALIZED READINESS POTENTIALS

To interpret the underlying mechanisms of behavioral effects on RTs, ERPs are helpful. As mentioned in the introduction, the interval between stimulus and LRP onset represents premotoric processes (i.e., perception and response selection); the interval between LRP and response onset represents motoric processes. Bisecting RTs using LRP onsets helps to confirm the functional loci of motor parameters. If motor parameters affect motoric processing, the LRP-R should be affected. On the other hand, if motor parameters affect premotoric processing, the S-LRP should be affected. Two experiments were conducted, manipulating different pairs of motor parameters.

3.1 Experiment 4: Motor Programming of Hand Placement and Response Sequence Length

3.1.1 Purpose

In the present study, hand placement and sequence length were manipulated as factors and observe their effects on RTs, P3 and LRPs.

3.1.2 Hypothesis

The hypothesis of the present study are as follows: first, both hand placement and sequence length were expected to affect RTs, showing slower responses in the longer

sequence conditions especially when hands are crossed. Second, no effects on the P3 nor S-LRP intervals were expected, suggesting both hand placement and sequence length do not affect perceptual or response selection. Third, longer LRP-R intervals were expected in both crossed-hand and longer sequence conditions, suggesting both manipulated factors affect motoric processes.

3.1.3 Method

Participants

Sixteen participants (seven female, mean age \pm SD 22.1 ± 2.8 yrs, one left-handed, handedness score (Oldfield, 1971) of 30, fifteen right handed, mean handedness score \pm SD of 83.3 ± 12.3), were recruited from Waseda University student population. All participants had normal or corrected-to-normal vision. Informed written consent was obtained before the experiment.

Stimuli

The kanji characters representing “left” or “right”, subtending approximately 0.31×0.31 degrees of visual angle served as imperative stimuli. They were randomly presented in white on a black background at the center of a cathode-ray tube display placed 75 cm in front of the participant. These stimuli were presented by a tachistoscope system (Iwatsu Isel Inc., IS-702), which also measured the RT as the interval between stimulus and index-finger response onsets. In the crossed-hand conditions, participants

placed one forearm on the table and another arm on a wooden shelf of 11 cm height. Response button boxes were also placed either on the table or on the shelf, respectively, for each responding hand. The placement of the forearms was exchanged in the second half of the experiment.

Procedure

Each trial began with the presentation of a fixation cross for 500 ms, after which it was replaced by one of the letters, remaining in view until a response occurred. Participants responded to the letters by pressing the left or right index finger, respectively, corresponding to the meaning of the letter. Intervals between a response and the next fixation point ranged between 2 and 3 s with incremental steps of 200 ms. An experimental session consisted of eight blocks of 60 trials each. The four conditions, resulting from the factor combinations of response sequence length (one button press with the index finger vs. three sequential button presses by index, ring, and middle finger, respectively) and hand placement (crossed vs. uncrossed hands) were administered in counterbalanced order across participants. Prior to each experimental condition, participant practiced the required response manner (i.e., combinations of hand placement and response sequence length) until he/she could smoothly perform it.

Recording

The electroencephalogram (EEG) was recorded from 128 sites with Ag/AgCl electrodes.

Horizontal electrooculograms (hEOG) were recorded from the left and right outer canthi, and vertical electrooculograms (vEOG) from above and below the left eye. These were recorded with DC to 205 Hz using a Biosemi Active Two system (Biosemi Inc.). All physiological signals were digitized at a rate of 1024 Hz.

Data Analysis

To obtain LRPs signals from lateral EEG (C3/C4) (Coles, 1989), for each response hand condition EEG signals at the ipsilateral recording site were subtracted from the signals from the homologous contralateral recording site. Separate mean difference waveforms were computed for trials requiring left- and right-hand responses. These difference waveforms were averaged separately for each participant and experimental condition. This subtraction procedure was employed to calculate S-LRP and LRP-R. The EEG was re-referenced to the average reference and corrected for ocular movement artifacts (Gratton, Coles, & Donchin, 1983). Trials with incorrect responses and EEG voltages exceeded a threshold of 100 μ V during the recording epoch were excluded from the analyses.

The P3 latency was determined as the time point when the ERP amplitudes reach positive peaks during the time window from 200 to 400 ms relative to a 100 ms baseline prior to imperative stimulus onsets. The LRP onset was determined as the intersection of the best fitting linear regression line through the slope of the LRP with the baseline (Mordkoff & Gianaros, 2000; Schwarzenau, Falkenstein, Hoormann, & Hohnsbein,

1998). The baseline was defined as the average voltage of the LRP during the 100 ms prior to stimulus onset for the S-LRP; and during the -650 to -550 ms before response onset for the LRP-R. The regression lines were calculated in jackknife averages, according to the procedure suggested by Miller, Patterson, and Ulrich (1998). When subjecting these onset measures to analyses of variance (ANOVA), F values were corrected as $FC = F / (n-1)^2$ (Ulrich & Miller, 2001).

3.1.4 Results

Behavioral results

Table 3-1 *Mean RT (ms), error rate (%), mean P3 intervals (ms), and mean LRP intervals (ms)*

	RT (SEM)	Error rate (SEM)	P3 latencies (SEM)	S-LRP intervals (SEM)	LRP-R intervals (SEM)
Uncrossed-Short	357.6 (6.3)	1.7 (0.4)	353.1 (11.2)	181.3 (1.3)	138.6 (0.5)
Uncrossed-Long	395.9 (8.5)	1.0 (0.2)	368.1 (11.7)	175.5 (0.7)	178.6 (0.7)
Crossed-Short	403.6 (10.3)	3.1 (0.6)	374 (13.2)	167.5 (0.9)	154.9 (0.4)
Crossed-Long	440.7 (9.5)	2.2 (0.5)	351 (11.4)	173.9 (1.5)	205.5 (1.2)

Table 3-1 gives the mean RTs and error rates. Repeated measures ANOVA revealed longer RTs in the crossed-hand condition ($M = 417$ ms) than in the uncrossed-hand condition ($M = 368$ ms), $F(1, 15) = 59.0, p < .01$, and longer RTs for the three sequential button press ($M = 410$ ms) than for one button press ($M = 375$ ms), $F(1, 15) = 55.7, p < .01$. No interaction was found, $F < 1$. For error rates, a main effect of hand placement, $F(1, 15) = 8.7, p = .01$, was found, indicating more errors when hands were crossed, whereas the sequence length effect did not reach significance, $F(1, 15) = 3.8, p = .07$. No interaction was found, $F < 1$.

P3 results

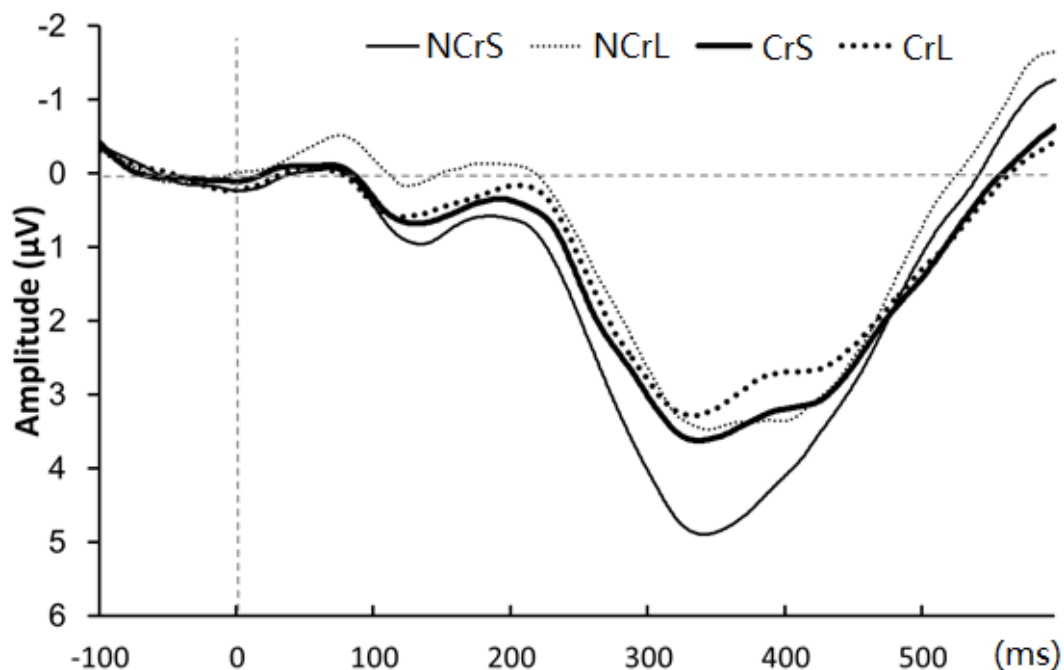


Figure 3-1. Grand averaged waveforms of P3. Stimulus onset is at time zero. Thin lines indicate Uncrossed-Short (dotted) and Uncrossed-Long (solid) conditions. Thick lines

indicate Crossed-Short (dotted) and Crossed-Long (solid) conditions.

Stimulus onset is at time zero. Thin lines indicate Uncrossed-Short (dotted) and Uncrossed-Long (solid) conditions. Thick lines indicate Crossed-Short (dotted) and Crossed-Long (solid) conditions.

As shown in Figure 3-1, neither hand placement nor sequence length affects the P3 latencies, $F < 1$. However, an interaction was observed between hand placement and sequence length, $F(1, 15) = 5.6, p = .03$.

LRPs results

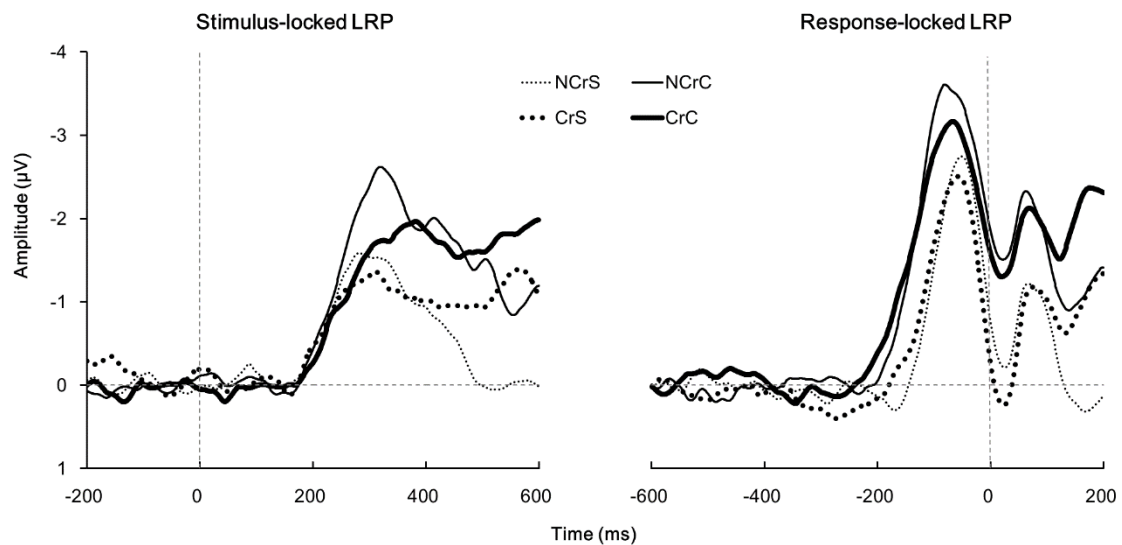


Figure 3-2. Grand averaged waveforms of LRPs. Stimulus onset is at time zero. Thin lines indicate Uncrossed-Short (dotted) and Uncrossed-Long (solid) conditions. Thick lines indicate Crossed-Short (dotted) and Crossed-Long (solid) conditions.

Repeated measures ANOVA of LRP-R intervals (Figure 3-2) revealed a main effect of hand placement, ($F_C(1, 15) = 6.9, p = .02$), with longer intervals for cross than uncrossed hands ($M = 180$ v.s. 159 ms). In addition, sequence length had a main effect, $F_C(1, 15) = 13.4, p = .00$, with sequences of button presses yielding longer intervals than single button presses ($M = 147$ v.s. 192 ms). No interaction was present, $F_C(1, 15) = 0.2, p = .65$. The S-LRP intervals were affected neither hand placement nor sequence length ($F_C < 1$). No interaction was observed ($F_C(1, 15) = 0.1, p = .7$).

3.1.5 Discussion

The present study investigated the temporal loci of hand placement effects in a sequential finger tapping task. Hand placement and response sequence length were orthogonally manipulated. Both factors independently prolonged RTs. For LRPs, both hand placement and sequence length resulted in longer LRP-R intervals, but did not affect the S-LRP intervals, suggesting motoric loci for both factors in choice RTs.

3.2 Experiment 5: Motor Programming of Movement Duration and Response

Sequence Complexity

3.2.1 Purpose

In the present study, two factors were orthogonally manipulated, which might influence motor programming, namely response sequence complexity and movement duration.

3.2.2 Hypothesis

According to predictions of the above-mentioned models including the AFM logic and characteristics of LRP, the following hypotheses were proposed.

First, both response sequence complexity and movement duration would affect RT, requiring more time for more complex and longer-duration conditions. Moreover, because two variables manipulated were motor-related, they should affect the LRP-R intervals but not the S-LRP intervals. Second, if response sequence and movement duration are programmed in parallel, as suggested in Klapp's two-process model, an underadditive effect of the two factors was expected on RT and the LRP-R intervals. Third, if response sequence and movement duration are programmed in separate modules, only additivity without any interaction of both factors was expected on RT and the LRP-R intervals, which is in accordance with Rosenbaum's HED model. Finally, if the motor programming stage is unitary, an overadditive interaction of response sequence complexity by movement duration should be observed in both RT and the LRP-R intervals.

3.2.3 Method

Participants

Thirty students from Waseda University participated in this study. Two participants were removed from analysis because of no measurable motor-related lateralization of ERPs.

Data of 28 participants (16 female; mean age \pm SD: 24.5 \pm 2.22 yrs; range: 20-29 yrs) was kept for further analysis. All participants were right-handed with mean handedness score of 84.8 (Oldfield, 1971), and had normal or corrected-to-normal vision. This study was approved by the Waseda University Ethics Committee. Written informed consent was obtained before the experiment.

Stimuli and Responses

White letters “L” or “R” with 1.5 cm height and 1.3 cm (visual angle of 0.9×0.7 degrees) width served as imperative stimuli. They were randomly presented at the center of the display against the black background of a computer monitor placed 1 m in front of the participant. The presentation of stimuli and recording of RTs and responses were controlled by a tachistoscope system (Iwatsu Isel Inc., IS-702).

Response sequences consisted either of three repeated presses with the index finger (simple) or of a sequence of index, ring, and middle finger presses (complex); the two conditions are the levels of factor complexity. A second factor (movement duration) consisted in requiring the last finger press to be either short or long (described below). The orthogonal combination of the factors response complexity and movement duration yielded four conditions.

Procedure

The experiment consisted of one session with the four conditions specified above,

presented block-wise. Each condition consisted of 30 practice trials, followed by two blocks of 48 test trials each. The order of conditions was counterbalanced across participants. In the practice trials, acoustic signals consisting of three consecutive sound clips were presented as instructions. In short and long duration conditions, clips lasted for 50-50-50 ms and 50-50-500 ms, respectively. During practice trials, participants were required to press buttons in the instructed sequence and approximate rhythms of the tones, alternating the responding hand after every trial. Compliance was visually monitored in the output signal of the keys. During test blocks each trial began with a plus symbol (1×1 cm) presented for 500 ms serving as fixation aid. It was replaced by either the letter “L” or “R”, which was shown until the first button was pressed. Letters were presented in a pseudo-random order. Intervals between a response and the next trial ranged between 2400 and 3500 ms with increments of 100 ms.

Recording

The EEG was recorded from 128 sites with Ag/AgCl electrodes. Vertical electrooculograms (vEOG) were recorded from above and below the left eye and horizontal electrooculograms (hEOG) from the left and right outer canthi. Both EEGs and EOGs were recorded with a bandwidth of DC to 205 Hz, using a Biosemi Active Two system (Biosemi Inc.). The mechanogram of each button press was also recorded through an analog input box connected to the Biosemi amplifier. All physiological signals were sampled at a rate of 1024 Hz.

Data Analysis

Only trials with correct responses and RTs ranging from 100 to 800 ms were analyzed.

In particular, duration errors were defined based on participants' third button presses. In the shorter duration conditions, participants should keep the duration of their last press under 500 ms, while in the long conditions, it was to be between 300 and 2500 ms¹.

Trials with fewer or more than three key presses, and/or intervals between key presses longer than 500 ms were excluded as errors. Trials with wrong orders of key presses or including muscular artifacts were also excluded from further analysis.

The EEG was re-referenced to the average reference and corrected for ocular movement artifacts using the algorithm described by Gratton et al (1983). The LRPs were computed from ERPs for left- and right-hand responses recorded from C3'/C4' (C18/B21 of the Biosemi electrode coordinate; approximately 1 cm above C3/C4, respectively) (Coles, 1989). For each response, the ipsilateral ERPs were subtracted from the contralateral ERPs relative to the responding hand. The difference waveforms were averaged across responding hands separately for each condition and participant. Two types of LRPs were calculated: The S-LRP synchronized to the onsets of the imperative stimuli and the LRP-R synchronized to response onsets.

¹ The criteria partially overlapped each other between the short and the long conditions ranging from 300 to 500 ms. Trials including such overlap were not excluded from analyses as errors. The percentage of such trials was 0.2% in the simple-short condition, 3.3% in the simple-long condition, 4.2% in the complex-short condition, and 3.1% in the complex-long condition, respectively. Given that a block-wise design was adopted, it was unlikely that participants committed duration errors on purpose; instead they did in fact comply with the task to program short and long responses, respectively at least in the overwhelming majority of trials.

Because amplitude differences in LRP waveforms was observed between conditions, it was not feasible to determine the LRP onset by applying either regression-based method (Mordkoff & Gianaros, 2000; Schwarzenau, et al., 1998) or relative criteria (Smulders, Kenemans, & Kok, 1996). Therefore, LRP onsets were measured by using an absolute criterion after applying the jackknife-based procedure (Miller, et al., 1998). Each averaged ERP was low-pass filtered off-line at 12 Hz (24 dB/oct). S-LRP intervals were measured relative to a pre-stimulus baseline (mean voltage during the 200 ms prior to stimulus onset) and LRP-R intervals were measured relative to a pre-response baseline (mean amplitude between –800 to –600 ms before response onset). The onsets of LRPs were determined as the time point when the LRP amplitude exceeded $-0.5 \mu\text{V}$. F -values were corrected as $F_C = F / (n-1)^2$ when applying the jackknife-based analysis of variance ANOVA (Ulrich & Miller, 2001). Repeated measures ANOVA with factors duration and response sequence complexity was applied to all dependent variables.

3.2.4 Results

Performance

Table 3-2 shows mean RTs on correct trials and mean error rates. Both response sequence complexity and movement duration affected RTs, showing longer RTs in the complex and long duration conditions. Supporting this observation, a two-way ANOVA revealed both significant main effects of response sequence complexity ($F(1, 27) =$

9.01, $p = .006$, $\eta p^2 = 0.25$) and of movement duration ($F(1, 27) = 4.53$, $p = .043$, $\eta p^2 = 0.144$). No interaction between factors was found ($F(1, 27) = 0.08$, $p = .78$, $\eta p^2 = 0.003$).

Table 3-2 Mean RT (ms), error rate (%), and mean LRP intervals (ms)

	RT (SEM)	Error rate (SEM)	S-LRP intervals (SEM)	LRP-R intervals (SEM)
Simple-Short	401 (16)	5.1 (1.1)	211 (3)	193 (3)
Simple-Long	414 (16)	5.2 (0.9)	204 (2)	214 (6)
Complex-Short	426 (16)	5.0 (1.5)	197 (3)	233 (6)
Complex-Long	439 (20)	6.3 (0.9)	181 (5)	303 (6)

For error rates, neither the main effect of sequence complexity ($F(1, 27) = 0.12$, $p = .734$, $\eta p^2 = 0.004$), movement duration ($F(1, 27) = 1.22$, $p = .279$, $\eta p^2 = 0.043$), nor the interaction was obtained ($F(1, 27) = 0.552$, $p = .464$, $\eta p^2 = 0.02$).

LRPs

Figure 3-3 shows grand-averaged LRP waveforms. The S-LRP intervals did not differ among conditions, although amplitudes appeared to be larger in the complex than in the simple conditions. The LRP-R intervals appeared to differ among conditions, showing longer LRP-R intervals in the complex and long duration conditions.

Table 3-2 shows mean LRP intervals measured with an absolute criterion after applying the jackknife procedure. A two-way ANOVA on mean S-LRP intervals neither showed main effects of response sequence complexity ($F_C(1, 27) = 1.96, p = .173$), movement duration ($F_C(1, 27) = 0.69, p = .415$), nor an interaction between these factors ($F_C(1, 27) = 0.09, p = .767$). In contrast, a two-way ANOVA on mean LRP-R intervals showed main effects of both response sequence complexity ($F_C(1, 27) = 7.12, p = .013$) as well as movement duration ($F_C(1, 27) = 5.24, p = .03$). However, no interaction was found ($F_C(1, 27) = 1.4, p = .246$).

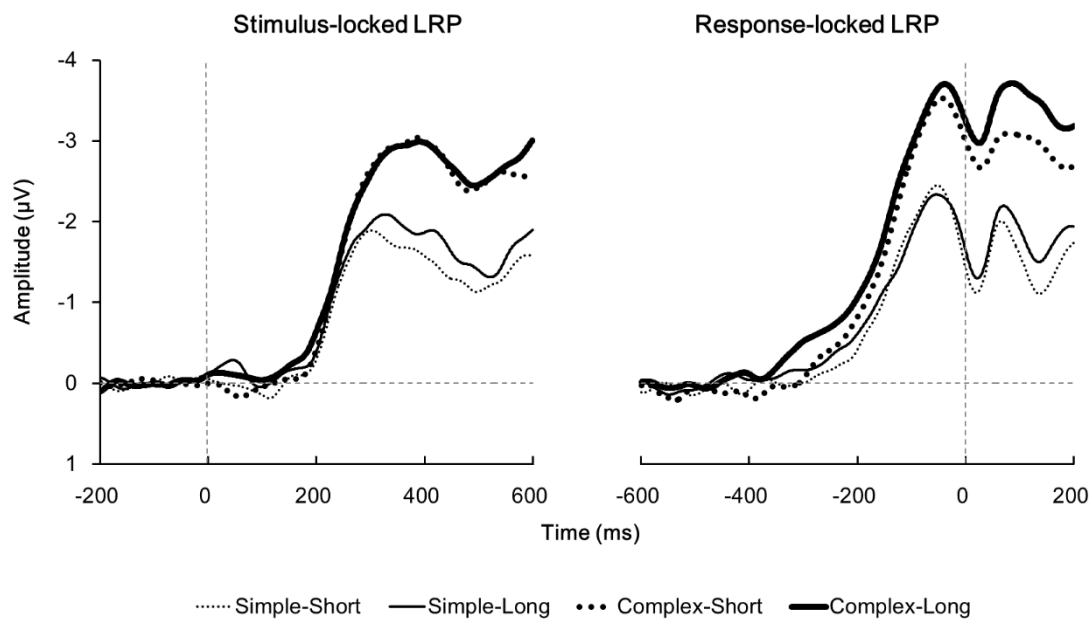


Figure 3-3. Grand averaged waveforms of LRP. Left: S-LRP waveforms. Stimulus onset is at time zero. Right: LRP-R waveforms. Response onset is at time zero. Thin lines indicate Simple-Short (dotted) and Simple-Long (solid) conditions. Thick lines indicate

Complex-Short (dotted) and Complex-Long (solid) conditions.

3.2.5 Discussion

The present study investigated whether the motor programming stage is a unitary stage or consists of several independent stages, orthogonally manipulating a pair of motor-related factors, namely, response sequence complexity and movement duration. RT results showed main effects of both factors but no interaction, suggesting the existence of two independent stages associated with response sequence complexity and movement duration. Both response sequence complexity and movement duration revealed additive effects in the LRP-R intervals, whereas neither factor affected the S-LRP intervals. Thus, electrophysiological evidence indicated two separate and independent motor processes located between response selection and overt responses.

3.3 Summary

Besides behavioral data, psychophysiological evidence (ERPs) was collected in two succeeding experiments. Participants performed choice RT tasks in both experiments, in which they responded to the stimuli for the left and right by tapping their left or right fingers, respectively, with different hand placement (crossed or uncrossed) and response sequence length (one or three) (experiment 4), or response sequence complexity (simple or complex) and movement duration (short or long) (experiment 5). All factors yielded main effects on RT but no interactions, supporting the existence of independent

substages suggested by experiments. Moreover, since the LRP is considered to be an index of hand-specific response activation. Specifically, the functional locus of the LRP onset is believed to follow response hand selection and at the beginning of motor programming. Additive effects of both pairs of parameters on the onsets of LRP-R, but not S-LRP, suggest motoric loci of those parameters. These findings are at variance with the notion of a unitary movement programming stage.

CHAPTER 4 NEURAL CORRELATES OF MOTOR PARAMETER SPECIFICATION: EVIDENCE FROM CONTINGENT NEGATIVE VARIATIONS

4.1 Experiment 6: Effect of Force Parameter Modification on the Contingent Negative Variation

4.1.1 Purpose

The purpose of present study was to further confirm the effect of the parameter modification that should be applied for the invariant motor program in terms of both central process and more peripheral process indexed by the CNV and the LRP, respectively. If the specification occurs at a more peripheral² level, the foreperiod LRP should be affected. On the other hand, if the specification is processed at a more central level, the late CNV should be affected. To obtain the LRP data, a target-force production task performed by both hands was adopted, unlike previous studies, in which the task was performed by only right hand (Masaki et al.1997; Masaki et al., 1998a).

4.1.2 Hypothesis

Since the CNV has been suggested to reflect central motor programming, it was expected to be sensitive to the need for variable versus invariant movement parameter specification.

² Note that the “peripheral” and “central” here referred to different levels in the hierarchy of information processing, not referred as terms in physiology.

4.1.3 Method

Participants

Eighteen male participants (mean age = 22.8 ± 2.3 years) were recruited from the university population. All participants were right handed and had normal vision.

Informed consent was obtained.

Procedure

The task was a target force production task using a precue procedure (Figure 4-1), in which the precue provided the participant with information about the response limb (right or left) and the required target force to be exerted. Two tasks were investigated: the single-target task (10 N) and the multiple-target task (4 N, 10 N, and 16 N).

Participant rested both forearms and palms comfortably on flat boards during the foreperiod to minimize any movements other than index finger responses. They were instructed to place their index fingers on left or right force keys. Participants performed 6 blocks of 63 trials each (including 5% catch trials to pre), which were separated by a short rest, and were assigned to either arrangement of the task (SMSMSM or MSMSMS). They were instructed to respond to the imperative stimulus by producing a target force with left or right index finger flexion but not to initiate a movement before the imperative stimulus appeared. Trials were presented with pseudo-randomized order resulting in the same order of responding hand between corresponding blocks of the

tasks. Isometric contraction was required to perform the task.

Each trial began with the presentation of a white fixation spot superimposed on a red horizontal bar in the open rectangle presented in the center of the CRT 100 cm in front of the participant. The visual angle subtended by the open rectangle was approximately $2.2^\circ \times 3.8^\circ$. The fixation spot remained visible until the offset of the imperative stimulus and both the red horizontal bar and the rectangle remained through a trial block. Precue information was added to the display 500 ms after fixation onset. In the single-target task, two white arrows appeared horizontally pointing either to the right or left side of the fixation spot as a precue. The right-directed precue indicated the right hand response, and vice versa. The height of the arrows was compatible to the force level. For instance, when the left upper arrows appeared pointing to the left, it required the 16 N force production with the left index finger flexion. The visual angle difference between centers of the precue square beside the fixation and the fixation spot was approximately 0.2° . In both tasks, two seconds after the presentation of the precue the white fixation spot became green signaling a response (i.e., the imperative stimulus).

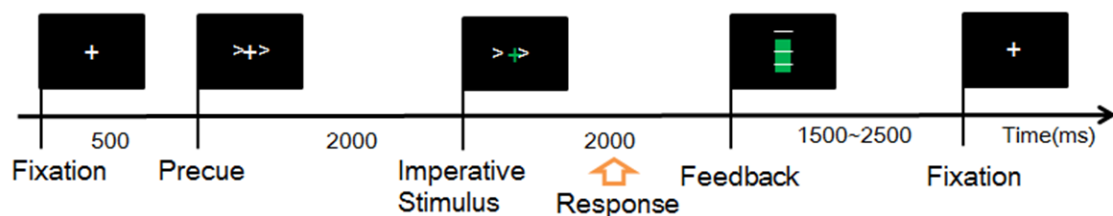


Figure 4-1. Procedure of precue paradigm adopted in the force production task

The participant was asked to correctly produce the target force as fast as possible but to avoid response error. The fixation spot disappeared with the response. To prevent premature responses, catch trials randomly appeared with a probability of 5 % in each block, in which the fixation spot became red after presentation of precue.

About three seconds after the response (ranging from 2500 to 3500 ms with an increment of 200 ms), a feedback signal was presented to provide knowledge of results and performance. A vertical green bar indicated the actual response force level. The white horizontal line in the single-target task indicated the 10 N force target, and the upper, middle, and lower white horizontal lines in the multiple-target task indicated 16 N, 10 N, and 4 N, respectively. Hence, the participants could determine the extent to which their force produced deviated from the target. Inter trial intervals (ITIs) were manipulated by presenting the feedback. In practice, the vertical bar in feedback was either red or blue. Blue bar suggested good performance, within 3.2 - 4.8 N for 4 N condition, 8 - 12 N for 10 N condition, and 12.8 - 19.2 N for 16 N condition, respectively. Red bar was shown when participant's performance was out of the target range.

Recording

The EEG was recorded from 128 sites with Ag/AgCl electrodes. Horizontal electrooculograms (hEOG) were recorded from the left and right outer canthi, and vertical electrooculograms (vEOG) from above and below the left eye. These were

recorded with DC to 205 Hz using a Biosemi Active Two system (Biosemi Inc.). All physiological signals were digitized at a rate of 1024 Hz.

Data Analysis

Performance. RT, peak force, and TTP force were measured for each subject. RT was measured from the imperative stimulus to the onset of the force curve. TTP was defined as the time between force curve onset and peak force. RT, force, and TTP of 10 N trials were subjected to paired sample t-test between simple- and multiple-tasks. Within each task, one-way ANOVA was applied with variable of target force. The 10 N trials in multiple-target task were matched with 10 N trials occurred at the same time in experimental sequence in the single-target task (Figure 4-2).

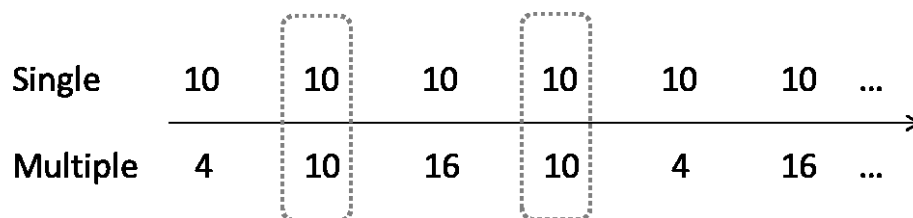


Figure 4-2. Match of 10 N trials between the single- and multiple-target tasks

CNV. The analysis period lasted 2000 ms from precue onset to imperative stimulus onset.

After artifact rejection was performed to eliminate trials containing dc-drift, head movement artifacts, or EOG amplitudes exceeding 100 μ V, artifact-free trials were averaged using the onset of the precue as a trigger. In the multiple-target task, only the 10 N target trials were averaged to compare with the single-target task across

corresponding blocks (i.e., the same responding hand). The CNV waveforms were digitally filtered with an 0.03 -12 Hz filter.

The CNV amplitudes were based on mean time intervals of 500 ms starting at the onset of the precue, referenced to a 200 ms mean voltage baseline before the precue. Thus, four amplitude measures were obtained (i.e., -2000 to -1500 ms, -1500 to -1000 ms, -1000 to -500 ms, and -500 to 0 ms). Each CNV amplitude measurement was subjected to three-way ANOVA with repeated measures on the variables of epochs (4) and electrodes (4) and tasks (2) (Greenhouse-Geisser Corrected). Where multiple comparisons were required, the Bonferroni test was employed.

Foreperiod LRP. Because rate of force development (i.e., TTP) was suggested to affect LRP (Masaki, et al., 2004; Ray, Slobounov, Mordkoff, Johnston, & Simon, 2000), only trials with TTP in the range of 70 – 140 ms were included in analysis for CNVs and LRPs. A two-step subtraction procedure was used to obtain LRPs (Gratton, et al., 1988). First must calculate the difference $D(t) = C3'(t) - C4'(t)$ at time t on each trial for both right- and left-hand responses. Next, the resulting difference waves were averaged over trials for left- and right-hand responses separately, and then averaged across hands after the wave for left-hand response was inverted in polarity: $LRP(t) = \{D(t) (\text{right hand}) - D(t) (\text{left hand})\}/2$. To average EEG the onset of precue was used as a trigger. The foreperiod LRP amplitudes were measured with the same procedure of the CNV. Each foreperiod LRP amplitude measurement was subjected to two-way ANOVA with

repeated measures on the variables of epochs (4) and tasks (2) (Greenhouse-Geisser Corrected). Where multiple comparisons were required, the Bonferroni test was employed.

4.1.4 Results

Performance

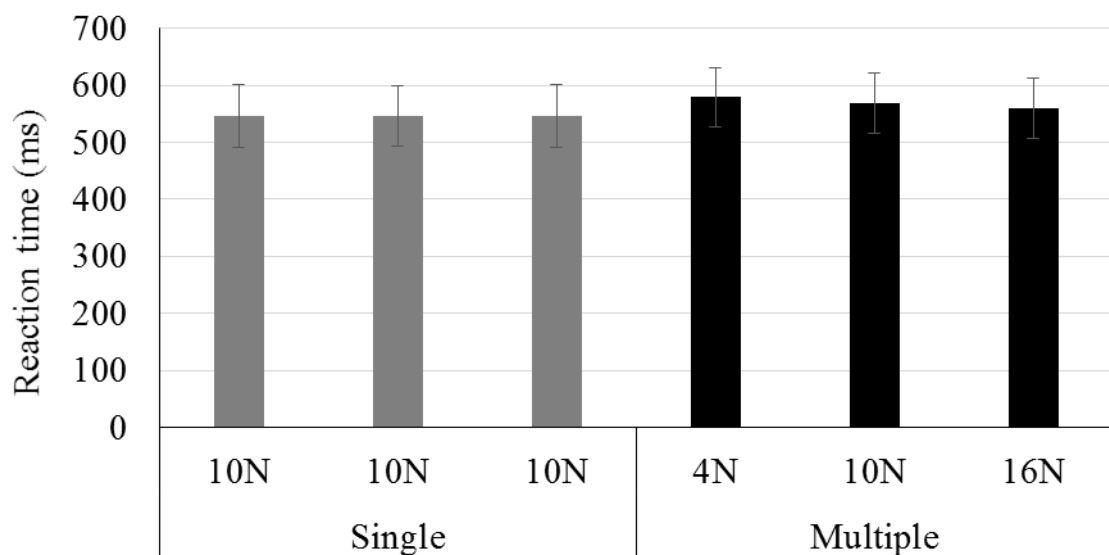


Figure 4-3. RTs in the single- and multiple-target tasks

Figure 4-3 showed results of RT in single- and multiple-target tasks. RTs of 10 N conditions did not differ between single- and multiple-target tasks ($t(1, 17) = -1.39, p = .18$). There was also no difference of RTs among three targets force conditions in either single- ($F(2, 51) = .00, p = 1.0$) or multiple-target task ($F(2, 51) = .035, p = .966$).

Figure 4-4 showed results of mean force in single- and multiple-target tasks. Paired t-test showed larger force of 10 N trials in the single- than in the multiple-target tasks ($t(1, 17)$). One-way ANOVA suggested significant difference among 4 N, 10 N, and 16 N trials ($F(2, 51) = 5231.3, p = .00$), but no difference among 10 N trials (matched with 4 N, 10 N, and 16 N in the multiple-target task respectively) in single-target condition ($F(2, 51) = .166, p = .85$).

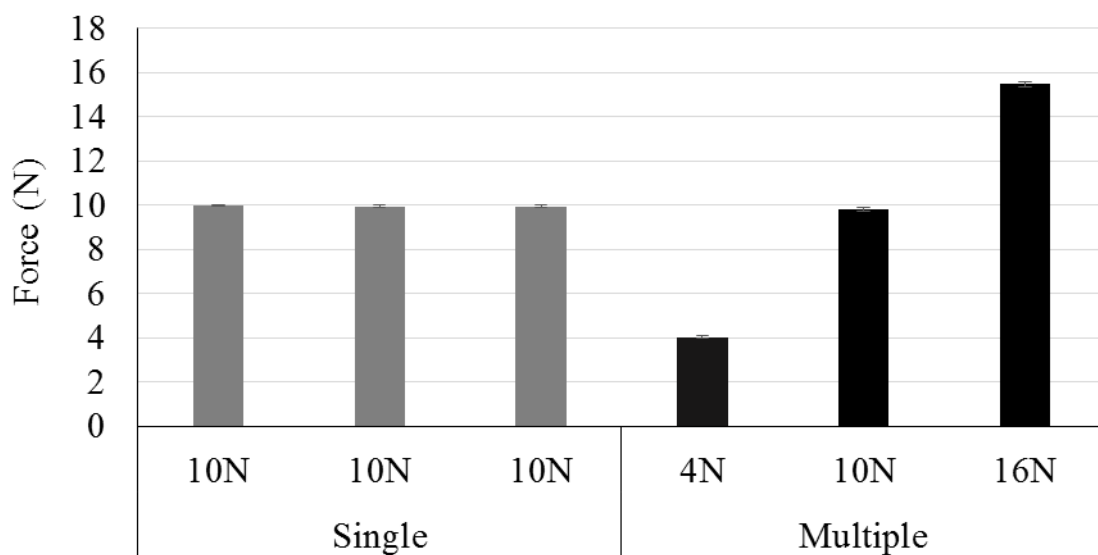


Figure 4-4. Exerted force in the single- and multiple-target tasks

Figure 4-5 showed results of mean TTP in single- and multiple-target tasks. No difference of TTP was found on 10 N trials between single and multiple tasks ($t(1, 17) = -1.094, p = .289$), or among 10 N trials in single-target task ($F(2, 51) = .017, p = .983$). However, the difference of TTP among 4 N, 10 N, and 16 N trials was significant in multiple-target task ($F(2, 51) = 8.283, p = .001$).

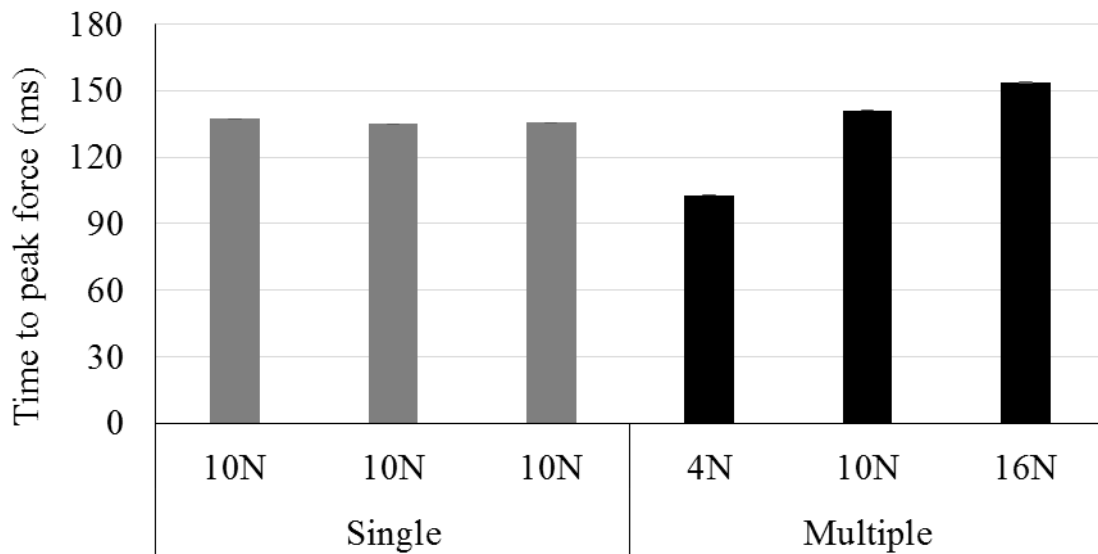


Figure 4-5. Time-to-peak force in the single- and multiple-target tasks

CNVs

The grand averaged CNVs at sites Fz, FCz, Cz, and Pz in the 10 N target trials for both tasks are depicted in Figure 4-6. The CNVs showed a frontal-central scalp distribution in both tasks. In addition, the steep negative deflections emerged immediately after the imperative stimulus, presumably reflecting preparation and execution of a specified motor response. ANOVA revealed main effects of epochs ($F(1, 17) = 10.92, p = .002, \varepsilon = 0.428, \eta p^2 = .39$), electrodes ($F(1, 17) = 6.36, p = .005, \varepsilon = .638, \eta p^2 = .27$), indicating more negative amplitudes at frontal and parietal than central regions especially in later epochs.

ANOVA also indicated interactions between epochs and electrodes ($F(9, 9) = 3.35, p = .038, \varepsilon = .26, \eta p^2 = .165$). More specifically, later epochs (-1500 ~ 0 ms) showed

more negative amplitudes than the first epoch (-2000 ~ -1500 ms) in frontal (Fz: $F(3, 15) = 10.54, p = .001, \eta p^2 = .678$) and parietal (Pz: $F(3, 15) = 9.85, p = .001, \eta p^2 = .663$) regions. At frontal-central regions (FCz), the second epoch (-1500 ~ -1000 ms) showed more negative amplitude than the first epoch ($F(3, 15) = 4.03, p = .027, \eta p^2 = .446$). At central regions (Cz), the two middle epochs (-1500 ~ -500 ms) showed more negative amplitudes than the first epoch ($F(3, 15) = 4.89, p = .014, \eta p^2 = .495$).

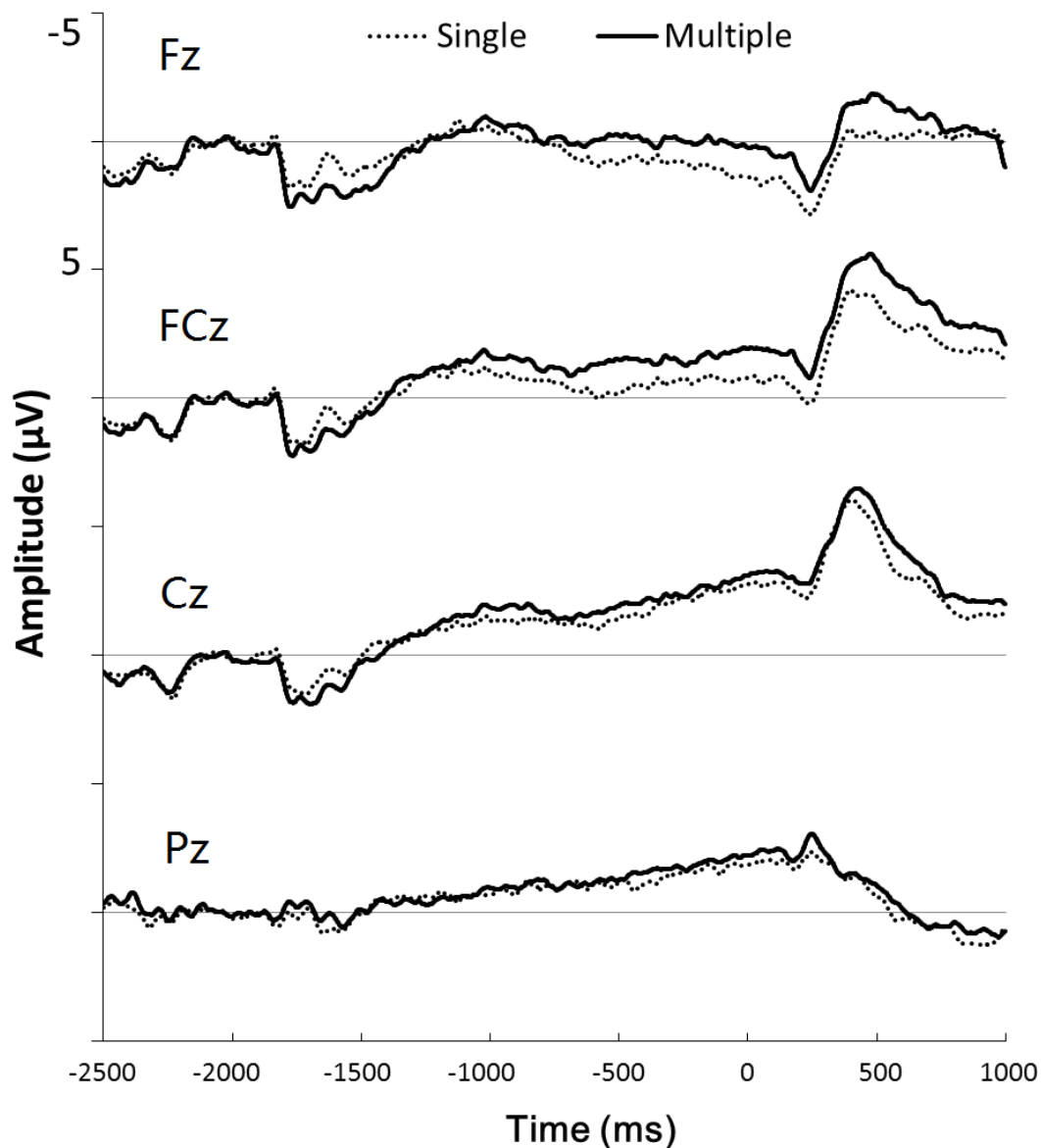


Figure 4-6. CNVs waveforms averaged from 10 N trials in the single- and multiple-target tasks. Dotted line indicates the single-target task. Solid line indicates the multiple-target task.

The most striking finding was, as can be seen in the Figure 4-6, that the late CNV was larger in the multiple-target task relative to that in the single-target task, even though the participants intended to produce the same target force across the two tasks. Although there was no main effect of tasks ($F(1,17) = 1.75, p = .20, \eta p^2 = .17$), an interaction between epochs and tasks was found ($F(1, 17) = 7.18, p = .005, \varepsilon = .549, \eta p^2 = .30$). Post hoc suggested more negative amplitude in the multiple-target than in the single-target task in later two epochs (-1000 to -500 ms: $F(1, 17) = 5.02, p = .039, \eta p^2 = .228$; -500 to 0 ms: $F(1, 17) = 7.73, p = .013, \eta p^2 = .313$). At the same time, more negative amplitude was found in later epochs (-1500 to 0 ms) than in the first epoch in both tasks ($p < .05$).

Figure 4-7 depicted the difference waveforms calculated by subtracting the CNVs in the single-target task from the multiple-target task. Larger waveforms were shown in the frontal regions before onsets of imperative stimulus. Topographies of the difference waveform also indicated more negativity in frontal regions especially in the left hemisphere.

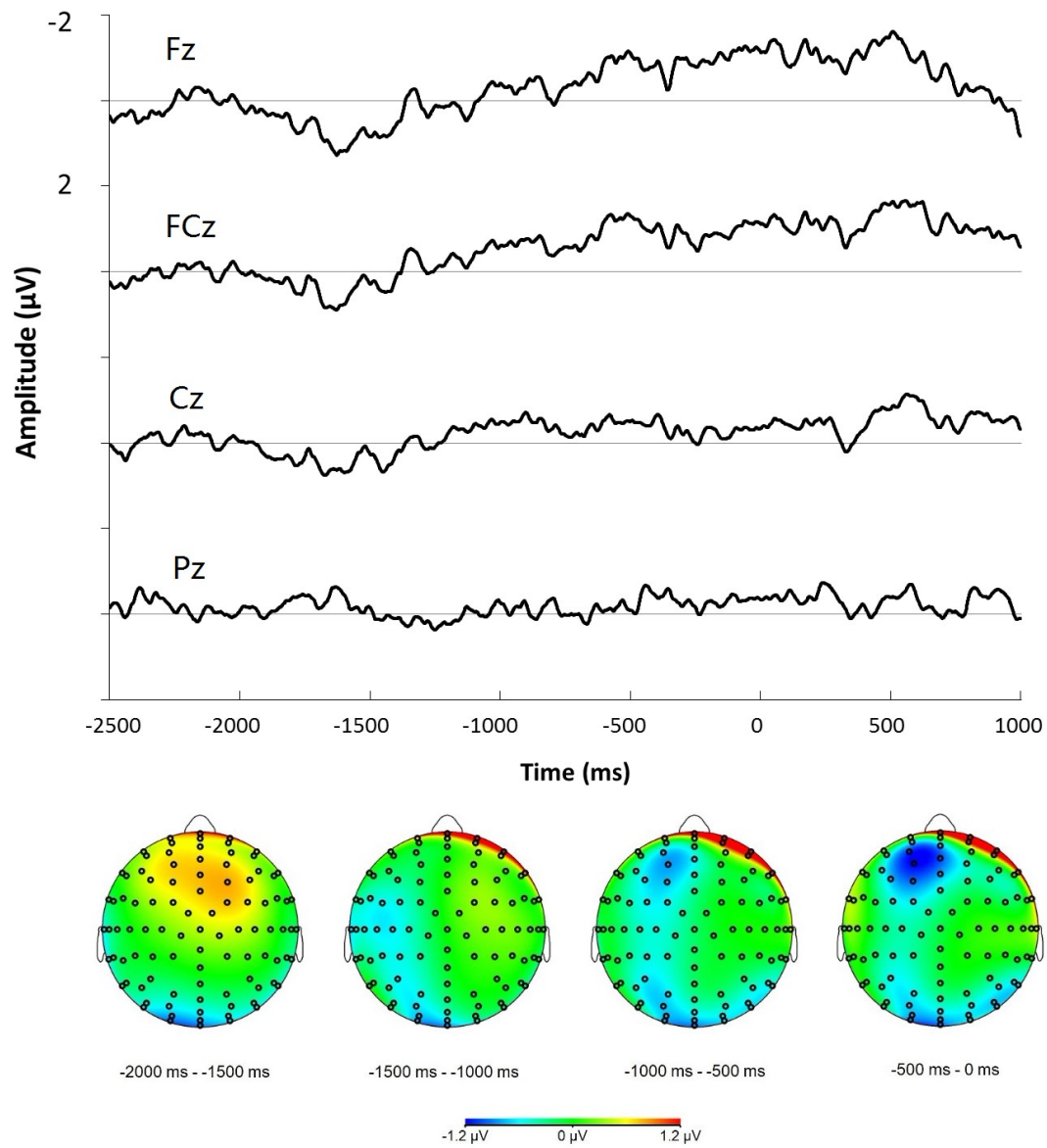


Figure 4-7. Difference waveforms and topographies calculated by subtracting the CNVs in the single-target task from the multiple-target task.

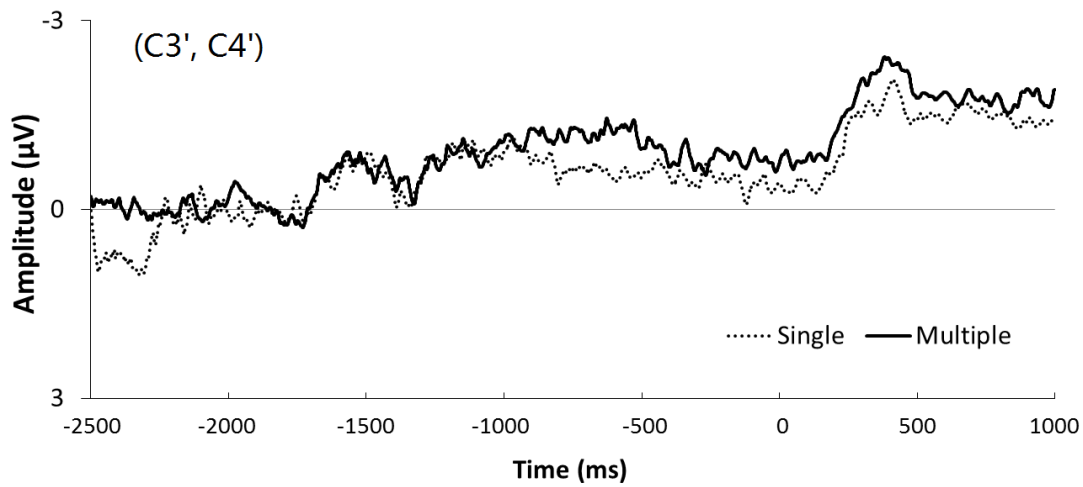


Figure 4-8. Foreperiod LRP waveforms averaged from 10 N trials in the single- and multiple-target tasks. Dotted line indicates the single-target task. Solid line indicates the multiple-target task.

Foreperiod LRP.

The grand averaged LRPs during the foreperiod in the 10 N force trials for both tasks are depicted in Figure 4-8. The foreperiod LRPs emerged after the precue onset in both tasks, indicating correct preparation for the response hand, and then retained the amplitude at a constant level during the foreperiod. After the imperative stimulus, the waveform became steeper in order to cross the response threshold (Gratton, et al., 1988). The foreperiod LRP was similar in both tasks from the precue to the response onset. For statistical analysis, the mean amplitudes of the foreperiod LRP were measured by averaging every 500 ms-interval during the foreperiod. Averaged foreperiod LRP amplitudes were referenced to a 500-ms baseline preceding precue onset. There were no significant differences in the foreperiod LRP amplitudes between tasks in any intervals.

4.1.5 Discussion

The main purpose of the present study was to clarify the effect of the force parameter modification on the movement-related process reflected in the CNV. The late CNV amplitude in the 10 N force production trial was larger in the multiple-target than in the single-target tasks, even though performance measures did not differ across the tasks. The waveform of the foreperiod LRP did not differ between tasks, consistent with the performance results. The observed CNV enhancement confirms previous reports examining the RP (Masaki et al., 1997; 1998a) and seems to further elucidate the effect of force parameter modification.

4.2 Summary

In sum, it was indicated that a central preparation system was mainly responsible for the force parameter modification process resulting in enhancement of the CNV. More peripheral preparation process indexed by the foreperiod LRP was not influenced by the force parameter modification. It suggests that the force parameter modification included in the later part of motor programming is processed in the context of an abstract form like the motor program (Schmidt, 1975; Rosenbaum, Saltzman, & Kingman, 1984).

CHAPTER 5 GENERAL DISCUSSION

The purpose of the present study was (1) to investigate how different motor parameters are organized during motor programming, whether it is a unitary stage with interactions between different kinds of parameters or whether each parameter is set independently of the others; (2) to confirm the functional loci of motor parameters during motoric processing; (3) to reveal the underlying neural mechanism of motor parameter specification. Six experiments were conducted to this aim.

Firstly, three experiments adopting the AFM logic were conducted to confirm potential motor-related parameters suggested by previous studies. Participants performed choice RT tasks in all the three experiments, in which they responded to the stimuli for the left and right by tapping their left or right fingers, respectively, with different movement duration (short or long), hand placement (crossed or uncrossed), or response sequence complexity (simple or complex). Three pairs of these parameters were orthogonally manipulated (experiment 1: movement duration and hand placement; experiment 2 and 3: movement duration and response sequence complexity). All factors yielded main effects on RTs but no interactions. These findings suggested the existence of separable independent substages associated with motor programming processes.

Secondly, besides behavioral data, psychophysiological evidence (i.e., ERPs) was collected in two succeeding experiments. Participants performed choice RT tasks in both experiments, in which they responded to the stimuli for the left and right by

tapping their left or right fingers, respectively, with different hand placement (crossed or uncrossed) and response sequence length (one or three) (experiment 4), or response sequence complexity (simple or complex) and movement duration (short or long) (experiment 5). All factors yielded main effects on RTs but no interactions, supporting the existence of independent substages suggested by previous experiments. Additive effects of both pairs of parameters on the onsets of LRP-R, but not S-LRP, suggest motoric loci of those parameters. These findings are at variance with the notion of a unitary movement programming stage.

Last, study 3 adopted a precue paradigm in a force production task to reveal the underlying neural mechanism of motor parameter specification. The precue stimulus provided the participants with information about both the response finger (right or left) and the required target force (4 N, 10 N, & 16 N). The participants were instructed to produce the target force of 10 N in the single-target task and to produce three different target forces in the multiple-target task. The late CNV amplitude was larger in the multiple-target task than in the single-target task, even though the same target force (10 N) trials were compared across the two tasks. In contrast, the LRPs during the foreperiod did not differ significantly between tasks. Since the CNV represents motor programming at a central level, it implies that force parameter specification is reflected by the CNV at a central level, rather than by the LRP at a peripheral level.

5.1 Organization Structures of Motor Programming

Accounting from the AFM

Previous studies suggested different substages during movement preparation (Arbib, Iberall, & Lyons, 1985; Sparks & Mays, 1983). According to the AFM logic (Sternberg, 1969), the additive effects of all manipulated factors on RTs in this study support the existence of at least three independent processes associated with hand placement, movement duration and response sequences during motor programming. This interpretation is supported by the LRP results that all factors separately affected the LRP-R interval, but not the S-LRP interval. The results of only main effects of all the manipulated parameters without interaction also suggest that no parallel processing occurred. Otherwise, underadditive effects of the two factors should be obtained.

It should be noted that there are several premises to apply the AFM logic (Sanders, 1998). First, one cannot apply the AFM to data when processing stages are overlapping each other in time; that is, stages must be assumed to be arranged in series and information transmission must be discrete. Second, the quality of stage output must not be impaired, and thus stage intactness should be invariant. Additionally, as Sternberg (2013) emphasized, previous studies that entertained doubts about the AFM logic did not follow the premises of the AFM. For example, stimulus displays should not be multiple or multidimensional. Other inappropriate variables include stimulus modality and age. The AFM also has problems to apply when choice RT is too long (i.e., 2 s). In

other words, interpretations based on the AFM logic should be valid unless the rules are broken.

Output intactness may be assumed from the rather low error rates in the present experiments, which did not show significant effects of the experimental factors. Therefore, one may conclude that each stage accomplished its function well and transmitted high-quality information to the next stage. Besides, the simple experimental manipulations in the present study relied on the original methodology of the AFM, that is, two factors were orthogonally manipulated, and the display of the stimuli was relatively simple.

Given that these premises hold, the additive results suggest the existence of at least three motoric substages associated with movement duration, hand placement and response sequences, respectively. One plausible interpretation might be that at least three factors affected the motor programming stage that might consist of a special structure, assembling three different motor-related parameters without any cross talk.

Most studies based on the AFM logic have manipulated factors that could be presumed to affect different stages (Sanders, 1998). Previous studies that orthogonally manipulated motor-related factors have shown additive effects of the manipulated factors (Spijkers & Walter, 1985; van Duren & Sanders, 1988). It seems that no psychophysiological study has orthogonally combined two motor-related factors based on the AFM logic. Besides, only a few studies have reported prolonged LRP-R intervals

(Osman et al., 1995; Leuthold et al., 1996; Low, et al., 2002; Masaki et al., 2004; Müller-Gethmann et al., 2000; Smulders, et al., 1995). Thus, the present study additionally shows at least three useful manipulations that affect motoric processes.

Accounting from HED Model

The results seem to support the hierarchical organization in motor control, and can be well explained by the HED model (Rosenbaum, et al., 1984; for a review, see Schröter & Leuthold, 2008). The basic assumption of the HED model is that the motor programs for response sequences are hierarchically structured before the imperative stimulus. In choice RT tasks, once the stimulus is identified, two processing phases occur one after another; both are controlled by the central component of HED model -- successive “unpacking” of nested subprograms. The first phase is the so-called *edit pass*, during which any uncertain response compositions are unpacked and specified hierarchically without physical execution. Then the *execution pass* starts, where the motor response program is unpacked into smaller elements that cannot be decomposed anymore, which are then executed successively.

The evidence for independent stages is in line with the HED model. Each of the experiments consisted of two motor-related dimensions. For example, in experiment 5, both movement duration and response sequence complexity were manipulated. Thus, combinations of these two factors resulted in four different conditions; the simple-short, the simple-long, the complex-short, and the complex-long conditions. In the

simple-short condition, response finger (index) was certain, and thus participants just needed to respond with the correct finger and hand as quickly as possible without considering the duration of key-press. Therefore, only the responding hand had to be specified as motor-related feature. In the simple-long condition, participants had to specify both response hand and movement duration. In the complex-short condition participants were also required to specify two features, both responding hand and fingers (index → index → ring). However, the motor specifications seemed to be more complicated in the complex-long condition. The participants had to specify responding hand, finger, and duration. Thus the number of motor features to be specified in the four conditions seemed to be one, two, two, and three, respectively. It is plausible that RT becomes longer as a function of the number of motor features. Because the design of the above mentioned experiments were similar to each other, the same logic derived from the HED model can explain the results.

Some Arguments

Spijkers and Steyers (1984) argued that movement duration can be preprogrammed in sliding movements. This assertion is at variance with the HED model. However, it is not in line with the results that movement duration affects RT and thus appears not to be preprogrammed (at least not fully). One possible explanation for the discrepancy between the present study and Spijkers and Steyers (1984) may be that in their study participants were instructed to prepare for the response in advance as early as possible,

whereas in the present study the participants were only instructed to respond to the stimulus as fast and accurately as possible.

The stimuli were kept constant throughout the presented three experiments, and near-identical main effects of movement duration were found. This seems to confirm the validity of duration as a motor-related parameter, even though only a single element of the processed sequence, either the first or the last element, was programmed.

One might argue that the additive effects on RT were due to the block-wise manipulation of conditions in this study. However, van Duren and Sanders (1988) have tested the interactions of three experimental variables, signal intensity, signal quality, and SRC in a two-choice reaction task under both blocked and mixed conditions. Although the effects of signal quality and SRC were smaller in the mixed condition, the additive effects of all the three variables were robust. Therefore, it is unlikely that the present additive effects would be very different in a mixed manipulation.

Moreover, according to another previous study (Schröter & Leuthold, 2008), responding hand is activated before the entire motor program is established. In the present study, the responding hand (left or right) was unknown before the imperative stimulus. Therefore, although participants had preliminary information about all other movement parameter, they could not establish the program until the responding hand was specified. Moreover, if participants could take full advantage from the block-wise design, the effects of motor parameters on RT should not have been observed. In other

words, the additive effects found were largely due to the valid manipulation of those motor-related factors.

5.2 Functional loci of Effects of Motor Parameters

Hand Placement

Results are in accordance with previous findings for hand placement (Brebner, et al., 1972; Brebner, 1973; Klapp, et al., 1979; Nicoletti, et al., 1984; Riggio, et al., 1986; Wallace, 1971, 1972) and for sequence length (Schröter & Leuthold, 2008; Smulders, et al., 1995). One of the most important findings in the present study is the confirmation of hand placement effect in processes of motor programming, as suggested by longer LRP-R but not S-LRP intervals. The present results extended previous findings of hand placement effects in psychophysiological studies (Leuthold & Sommer, 1998; Ragot, 1984).

Ragot (1984) investigated hand placement effects in two different tasks. In experiment one, participants were asked to perform a choice RT task, in which they pressed buttons with hands being either crossed or uncrossed. Another factor manipulated was stimulus location. Results showed that the P3 latency was only affected by the stimulus location, but not by hand placement, suggesting that hand placement did not affect stimulus-response matching. In the second experiment, participants extended or flexed the left or right index fingers at their own pace with

hands being either crossed or uncrossed. The BP did not differ between conditions. The null effects of hand placement on the BP might be due to the experimental paradigm. Because participants voluntarily performed the tasks, they had enough time to prepare the movement even with their hands crossed.

In a later study, Leuthold and Sommer (1998) asked participants to perform a force production task with hands either crossed or uncrossed. Another factor manipulated was stimulus brightness, which was considered to affect the process of stimulus evaluation. Results showed longer RTs when participants' responding hands were crossed than uncrossed, no matter whether stimuli were bright or dim. The P3 latencies were affected by the stimulus brightness but not by hand placement, suggesting that hand placement did not affect stimulus evaluation. The unaffected P3 latency by hand placement was in consistent with Ragot's results (1984).

The present study extended previous findings in several aspects. First, compared with the P3, which is superimposed by some other components, the LRP as a difference waveform can be a better tool to investigate cognitive issues (Luck, 2005). Thus the findings on the LRPs provided a more solid and confirmed proof of the temporal locus of hand placement effect. Second, the prolonged LRP-R interval with crossed-hands indicated the effects of hand placement on motor-related potentials which were not manifested in Ragot's study (1984). Third, in the present experiment, the stimuli were presented only in the center of the monitor, not shown peripherally to the fixation as in

previous studies (Leuthold & Sommer, 1998; Ragot, 1984). Thus the effect of stimulus position was eliminated in the present study. In this case, the processing of hand placement would not be affected by an earlier processing of stimulus position.

Another new finding in the present study is the robust and stable hand placement effects in both the single button press (RT: 45 ms; LRP-R: 28 ms) and the long sequence conditions (RT: 45 ms; LRP-R: 25 ms). Since only effects of hand placement and sequence length were found on both RTs and LRP-R intervals, without any interactions between the two factors. It may conclude that their effects are independent each other during processes of motor programming. A possible explanation for the identical hand placement effects between the short and the long sequence conditions might be that participants prepared the three button presses in a chunk. Once they decided the responding hand, the processing of hand placement was finished and would not be affected by the length of sequence any more.

One may notice that there is a discrepancy of hand placement effects between RTs and LRP intervals (i.e., smaller effect size for LRP intervals). One reason might be the measurement of LRP intervals using averaged waveforms (measured under each condition and across subjects). A more elegant design with more temporal indices might be helpful to figure out if any other processes are affected by hand placement.

Response Sequences

The observed main effects on RTs are also in accordance with previous findings and for sequence length (Schröter & Leuthold, 2008; Smulders, et al., 1995), and response sequence complexity, which observed longer RTs for more complex finger tapping conditions (Leuthold & Schröter, 2011). This result is in agreement with the prediction of Rosenbaum's HED model (Rosenbaum et al., 1984; 1987). According to the HED model, RT is affected by the time consumed by unpacking motor programs into decomposable elements. The more elements to unpack and execute, the longer RT.

In this study, all tasks included sequential actions. Specifically, in the simple conditions, participants pressed one button three times with the index finger only, while in the complex conditions, they pressed three different buttons with their index, ring, and middle fingers, respectively. Thus, only the index finger movement was unpacked in the simple conditions, whereas three fingers had to be specified (unpacked) in the complex conditions, resulting in the effect of sequence complexity on RTs.

The effect of response complexity on the LRP-R intervals was consistent with Smulders et al.'s previous findings (1995). They manipulated both stimulus degradation and response complexity in a choice RT task. The manipulation of complexity was between one single press by the index finger, and three presses by the index, ring, and middle fingers, respectively. They found longer LRP-R intervals in the more complex condition. Results in the present study extended their findings by reconfirming the response complexity effect on the LRP-R intervals with sequence length being

controlled for. Moreover, the prolonged LRP-R interval in this study supports the motoric locus of the response sequence effects.

Movement Duration

One of the purposes was to investigate the locus of the movement duration effect. Previous research has shown additive effects of movement duration and foreperiod on RT (Spijkers & Steyvers, 1984); however, due to the uncertain locus of the foreperiod effect, the functional locus of the movement duration factor remained unclear. An effect of movement duration in the present study was not found in the S-LRP interval but only in the LRP-R interval, suggesting a motoric locus of this factor.

The effect of movement duration on RTs in the present study is also consistent with the previous findings of Spijkers and Steyvers (1984) and Leuthold and Jentzsch (2011). Magnuson, Robin, and Wright (2008) found no effect of movement duration on RTs. Their participants were required to tap a key either once or four times repetitively, with either 150 ms or 450 ms duration, orthogonally manipulating sequence number and tapping duration. However, the null effect of duration in their study might be due to their self-select paradigm (see also Immink & Wright, 2001), where participants had enough time to learn and preprogram the required sequence before its execution.

Hackley and Miller (1995) observed larger foreperiod LRP amplitude in the complex than in the simple condition when responding hand was specified by the

precue. Smulders et al. (1995) further revealed that there were no complexity effects on amplitudes until a certain time point after the LRP onsets. These findings imply that responding hand is selected before specification of the other motor parameters in complex movement production. In the present study participants did not have sufficient time to preprogram the sequence, because they did not know the hand of response in advance. In addition, although each sequence included three elements and required an index-finger press as common first element for all conditions, only the last element (i.e., duration of the middle-finger press) differed between the short and long duration conditions. Nevertheless, a robust effect of movement duration was obtained on RTs, indicating that participants separately programmed sequences and durations in a chunk prior to response initiation. The main effect of movement duration in this study also supports the assertion of Klapp (1995, 2003) that the INT process cannot be preprogrammed in choice RT tasks.

However, it is ambiguous how these independent stages are structured. Keele (1981) suggested that the increased time demands of programming of slower movement might be due to a longer interval between onsets of accelerative and decelerative forces. This assumption was tested by a study, in which a pronounced effect of movement duration was found on the timing of EMG activity (Wallace & Wright, 1982). These studies suggest that movement duration should affect a stage associated with response execution including motor adjustment. However, in a previous study that adopted a

precue paradigm in a sliding movement task, researchers found an under-additive interaction between duration uncertainty and direction uncertainty, suggesting a parallel processing of duration and direction (Spijkers & Steyvers, 1984). The present results cast doubt on the controversial functional loci of movement duration effects. It is noteworthy that in experiment 3 the first two elements of response sequence were kept constant (same fingers and same duration) but varied the last element. Nevertheless, a duration effect was found on RT. Therefore, the functional locus of the duration effect cannot be due to the motor adjustment stage.

5.3 Central Representations of Motor Parameter Specifications

Several studies have reported larger movement-related potentials (i.e., the CNV and the RP) with larger forces exerted (Hink, Deecke, & Kornhuber, 1983; Kristeva, Cheyne, Lang, Lindinger, & Deecke, 1990; Kutas & Donchin, 1977). However, these findings suggest that a larger force production than that used in the present study may be necessary to enlarge the amplitude of the movement-related potentials. For example, Kutas and Donchin (1977) asked participants to produce force levels ranging from 5 to 20 kgf (approximately 49 - 196 N). Obviously, the CNV augmentation observed in the multiple-target task in the present study cannot be ascribed to the preset target force (i.e., 10 N) and mean exerted force difference between tasks. Since only 10 N trials between the single- and multiple-target tasks were compared.

Previous studies using a target force production task have confirmed enhanced RP

when the participants had to apply a different force parameter for the motor program every trial (Masaki et al., 1997; 1998a). In the present study, a similar effect on the late CNV in the multiple-target task was also observed by a comparison between the 10 N force production trials in two tasks. The participant was able to prepare for the response during the foreperiod since the target force was informed by the precue in both tasks. Theoretically, with the multiple-target task, the existing motor program for flexion of the index fingers could be retained, but only force parameter modification was required. In addition, the motor program for execution of the flexion of the index fingers was common across response hands and tasks in this study. Thus, the functional difference between the two tasks was whether the participant had to apply a different force parameter for the motor program every trial (the multiple-target task) or not (the single-target task). Hence, it is reasonable to conclude that the late CNV enhancement found in the multiple-target task can be attributed to the process of the force parameter modification.

Some researchers have emphasized that the foreperiod LRP amplitude in the precue paradigm is an important index of peripheral motoric parameterization, because it increases with amount of advance information determining the forthcoming response manner (e.g., Leuthold, et al., 1996; Ulrich et al., 1998). These findings about the foreperiod LRP provided some evidence for a hierarchical view of movement preparation (Rosenbaum, 1980, Ulrich et al., 1998). On the other hand, the CNV

steadily developed as a function of the amount of advance information. MacKay and Bonnet (1990) also found that the CNV at postcentral region became systematically larger with increasing precue information using a similar paradigm as Ulrich et al. (1998). These findings suggest that the CNV might reflect the central programming which integrates advance information into a single code, and the foreperiod LRP amplitude might reflect more peripheral preparation after the integration (Ulrich et al., 1998). They proposed the two-phase model that the CNV may reflect the assembling of a motor program and the foreperiod LRP may represent implementation of it.

In this study, the amplitude of the CNV increased reflecting force parameter modification, but the foreperiod LRP did not. These results suggest that central preparation process but not peripheral preparation process represents the force parameter modification. Full information precue seemed to have no effect on the foreperiod LRP in either task, resulting in similar integration processes for advance information and peripheral preparation processes. In addition, earlier onset of the foreperiod LRP than the CNV enhancement indicates that force parameter modification is processed even after the accomplishment of hand preparation which awaits the terminal response parameterization. Thus, it is plausible that the force parameter modification was handled by the central preparation process in an abstract form preceding the final response execution process in a peripheral level.

Previous studies using precue methods showed that CNV amplitude increased with

the amount of advance information measured at postcentral region (MacKay & Bonnet, 1990) or over centroparietal region (Ulrich et al., 1998), suggesting that the motoric process was responsible for the enhancement. Contrary to these findings, the effect of force parameter modification was distributed more broadly (i.e., not only over centroparietal but also over frontal) in the present study. Since the paradigm included only full information precue unlike previous studies, any differences due to the advance information presented by the precue is not involved in the present results. It also seems unlikely that the increased CNV could be ascribed to different anticipations of the imperative stimulus (e.g., van Boxtel & Brunia, 1994), because the informative value of the imperative stimuli was identical between tasks.

If, as Ulrich et al (1998) suggested, the centroparietal effect is due to the enhanced RP, the slightly different distribution of the enhanced CNV in this study does not seem simply due to motoric processes. However, previous reports have suggested that the RP may also increase with motivation (McAdam & Seales, 1969) and effortful process (Masaki, Takasawa, & Yamazaki, 1998b). In the latter study, the RP was larger even at frontal region on trials in which the participants pulled a trigger in an attempt to produce a target force compared to the RP on trials in which they simply pulled the trigger without a target, suggesting involvement of effortful processing. Thus, it is possible that the force parameter modification in the central preparation system required effortful processing, leading to an increased CNV.

Advantages of the CNV paradigm include the ability to manipulate information about the forthcoming task as conveyed by the precue (Rosenbaum, 1980) and the ability to clarify the temporal affection of the parameter modification on the motor-related process due to its fixed interval between the precue and the imperative stimulus. The significant increase of the CNV in the present study lasted for longer ranges (i.e., starting about 1000 ms before the response) than that of the RP (i.e., starting 400 ms before the movement; Masaki et al, 1997). It is likely that this discrepancy is due to methodological differences between paradigms. In the present study, the precue might allow the participants to promptly handle the motor programming during the foreperiod. On the other hand, as indicated in the results of a previous study which used a self-paced movement resulting in longer inter-trial intervals more than about 20 s, the motor program and parameterization might be built up immediately before the movement, because the motor program is difficult to retain during such longer periods (e.g., Adams, & Dijkstra, 1966).

5.4 Conclusion

In conclusion, the present study suggests that (1) motor programming stage consists of separable independent substages associated with various motor parameters; (2) functional loci of these motor parameters are in motoric processes after response hand selection; (3) specification of such motor parameters occurs at a central rather than peripheral level.

5.5 Limitation and Perspectives

Some studies have asserted that additive effects do not provide solid evidence for independence of stages, because it is possible that the influence of manipulated factors on a common stage also results in additive effects. Sternberg (2013) himself recently suggested that additivity supports but does not imply serial, discrete, independent stages because in principle other models, such as cascade models (McClelland, 1979) are also able to produce additive effects. Therefore it is conceded that the suggestion of several independent motor programming stages must be tentative and await further corroboration by additional evidence or explicit modelling.

Another basic problem in drawing conclusions from the absence of interactions (i.e. additivity) is that it implies arguing for the null hypothesis. However, main effects of each factor were found, demonstrating that the absence of an interaction was not likely due to a lack of power. In addition, if both factors affect a unitary stage in parallel, one would expect an under-additive interaction between the two factors. This was not the case in the present study. Therefore, the present findings are at least in line with the suggestions made previously by Sanders that motor processes are separable.

Moreover, the present results did not provide us with enough information about the order of processes associated with motor parameters. Studies using other approaches (e.g., Rosenbaum's precue paradigm, Rosenbaum, 1980; 1983) might be helpful to reveal the sequence of movement parameter assembling. For example,

Müller-Gethmann et al. (2000) manipulated movement direction and response force in a precue paradigm. Precues provided either no information or partial information about either movement direction or response force. They found that advance information about both factors shortened the S-LRP intervals, while advance information about only movement direction, rather than response force, shortened the LRP-R intervals. They concluded that response force is specified prior to movement direction.

Another limitation of the present study might be the brain mechanism of motor programming. Neurophysiological and neuropsychological studies indicate that the supplementary motor area (SMA) and pre-SMA play a key role in temporal sequencing movements (Halsband, Ito, Tanji, & Freund, 1993; Gerloff, Corwell, Chen, Hallett, & Cohen, 1998; Kennerley, Sakai, & Rushworth, 2004; for a review, see Tanji, 2001). Besides, both the SMA and the primary motor cortex (M1) have been demonstrated to be influenced by sequence complexity of responses (Gerloff et al., 1998; Leuthold & Schröter, 2011). It is believed that during the processing of movement production, the information flows from pre-SMA to SMA, then from SMA to M1 (Lee, Chang, & Roh, 1999).

The technique of ERPs provides excellent temporal resolution, but is poor at spatial resolution because of volume conduction. Therefore, the present study cannot specify precise brain regions responsible for programming of the motor parameters. Future studies using microelectrode measures (single-unit and local field-potential recordings)

or hemodynamic measures (positron emission tomography, PET, and functional magnetic resonance imaging, fMRI) might be helpful to reveal the brain mechanism of motor programming.

REFERENCES

- Adams, J. A., & Dijkstra, S. (1966). Short term memory for motor responses. *Journal of Experimental Psychology*, *71*, 314-318. doi: 10.1037/h0022846
- Adams, J. A. (1971). A closed-loop theory of motor learning. *Journal of Motor Behavior*, *3*(2), 111-150. doi:10.1080/00222895.1971.10734898
- Arbib, M. A., Iberall, T., & Lyons, D. (1985). Coordinated control programs for movements of the hand. *Hand function and the neocortex*. In A.W. Goodwin, & I. Darian-Smith (Eds.), *Experimental Brain Research Supplement*, (Vol. 10, pp. 111–129). New York: Springer.
- Brebner, J. (1973). SR compatibility and changes in RT with practice. *Acta Psychologica*, *37*(2), 93-106. doi: 10.1016/0001-6918(73)90023-1
- Brebner, J., Shepard, M., & Cairney, P. (1972). Spatial relationships and S-R compatibility. *Acta Psychologica*, *36*, 1-15. doi: 10.1016/0001-6918(72)90040-6
- Brunia, C. H. (2003). CNV and SPN: Indices of anticipatory behavior. In *The Bereitschaftspotential* (pp. 207-227). Springer US. doi: 10.1007/978-1-4615-0189-3_13
- Callan, J., Klisz, D., & Parsons, O. A. (1974). Strength of auditory stimulus-response compatibility as a function of task complexity. *Journal of Experimental Psychology*, *102*(6), 1039. doi: 10.1037/h0036329
- Coles, M. G. (1989). Modern mind - brain reading: Psychophysiology, physiology, and

- cognition. *Psychophysiology*, 26(3), 251-269. doi:
10.1111/j.1469-8986.1989.tb01916.x
- Coles, M. G. H., & Rugg, M. D. (1995). Event-related potentials: An introduction. In M. D. Rugg, & M. G. H. Coles (Eds.), *Electrophysiology of Mind: Event-related brain potentials and cognition* (pp. 1-26). Oxford: Oxford University Press.
- Eriksen, C. W., & Schultz, D. W. (1979). Information processing in visual search: A continuous flow conception and experimental results. *Perception & Psychophysics*, 25(4), 249-263. doi: 10.3758/BF03198804
- Fitts, P. M., & Deininger, R. L. (1954). S-R compatibility: Correspondence among paired elements within stimulus and response codes. *Journal of Experimental Psychology*, 48, 483-492. doi: 10.1037/h0054967
- Fitts, P. M., & Seeger, C. M. (1953). S-R compatibility: Spatial characteristics of stimulus and response codes. *Journal of Experimental Psychology*, 46, 199-210. doi: 10.1037/h0062827
- Gerloff, C., Corwell, B., Chen, R., Hallett, M., & Cohen, L. G. (1998). The role of the human motor cortex in the control of complex and simple finger movement sequences. *Brain*, 121(9), 1695-1709. doi:10.1093/brain/121.9.1695
- Gratton, G., Coles, M. G. H., & Donchin, E. (1983). A new method for off-line removal of ocular artifacts. *Electroencephalography and Clinical Neurophysiology*, 55, 468-484. doi: 10.1016/0013-4694(83)90135-9
- Gratton, G., Coles, M. G., Sirevaag, E. J., Eriksen, C. W., & Donchin, E. (1988).

- Pre-and poststimulus activation of response channels: A psychophysiological analysis. *Journal of Experimental Psychology: Human perception and performance*, 14(3), 331. doi: 10.1037/0096-1523.14.3.331
- Hackley, S. A., & Miller, J. (1995). Response complexity and precue interval effects on the lateralized readiness potential. *Psychophysiology*, 32(3), 230-241. doi: 10.1111/j.1469-8986.1995.tb02952.x
- Halsband, U., Ito, N., Tanji, J., & Freund, H. J. (1993). The role of premotor cortex and the supplementary motor area in the temporal control of movement in man. *Brain*, 116(1), 243-266. doi:10.1093/brain/116.1.243
- Henry, F. M., & Rogers, D. M. (1960). Increased response latency for complicated movements and a "memory drum" theory of neuromotor reaction. *Research Quarterly of the American Association for Health, Physical Education, & Recreation*, 31, 448-458. doi:10.1080/10671188.1960.10762052
- Hink, R. F., Deecke, L., & Kornhuber, H. H. (1983). Force uncertainty of voluntary movement and human movement-related potentials. *Biological Psychology*, 16, 197-210. doi: 10.1016/0301-0511(83)90024-8
- Ilan, A. B., & Polich, J. (1999). P300 and response time from a manual Stroop task. *Clinical Neurophysiology*, 110(2), 367-373. doi: 10.1016/S0168-5597(98)00053-7
- Immink, M. A., & Wright, D. L. (2001). Motor programming during practice conditions high and low in contextual interference. *Journal of Experimental Psychology-Human Perception and Performance*, 27(2): 423-437. doi:

10.1037/0096-1523.27.2.423

Inhoff, A., Rosenbaum, D., Gordon, A., & Campbell, J. (1984). Stimulus-response compatibility and motor programming of manual response sequences. *Journal of Experimental Psychology: Human Perception and Performance*, *10*, 724-733. doi:

10.1037/0096-1523.10.5.724

Kennerley, S. W., Sakai, K., & Rushworth, M. F. S. (2004). Organization of action sequences and the role of the pre-SMA. *Journal of neurophysiology*, *91*(2), 978-993.

doi: 10.1152/jn.00651.2003

Keele, S. W. (1968). Movement control in skilled motor performance. *Psychological Bulletin*, *70*(6), 387-403. doi: 10.1037/h0026739

Keele, S. W. (1981). Behavioral analysis of movement. In V. Brooks (Ed.), *Handbook of physiology: Sec. 1. The nervous system: Motor control*. (Vol. 2, pp. 1391-1414).

Bethesda, MD: American Physiological Society. doi: 10.1002/cphy.cp010231

Keele, S. W., & Summers, J. J. (1976). The structure of motor programs. In: G.E.

Stelmach (ed.) *Motor control: Issues and trends*, 109-142. New York: Academic.

Kelso, J. A. S. (1977). Motor control mechanisms underlying human movement production. *Journal of Experimental Psychology: Human Perception and*

Performance, *3*, 529-543. doi: 10.1037/0096-1523.3.4.529

Klapp, S. T. (1995). Motor response programming during simple choice reaction time: The role of practice. *Journal of Experimental Psychology: Human Perception and*

Performance, *21*(5), 1015-1027. doi: 10.1037/0096-1523.21.5.1015

- Klapp, S. T. (2003). Reaction time analysis of two types of motor preparation for speech articulation: Action as a sequence of chunks. *Journal of Motor Behavior*, 35(2), 135-150. doi: 10.1080/00222890309602129
- Klapp, S. T., & Erwin, C. I. (1976). Relation between programming time and duration of the response being programmed. *Journal of Experimental Psychology: Human Perception and Performance*, 2, 591-598. doi: 10.1037/0096-1523.2.4.591
- Klapp, S. T., Greim, D. M., Mendicino, C. M., & Koenig, R. S. (1979). Anatomic and environmental dimensions of stimulus-response compatibility: Implication for theories of memory coding. *Acta Psychologica*, 43(5), 367-379. doi: 10.1016/0001-6918(79)90031-3
- Klapp, S. T., Wyatt, E. P., & Lingo, W. M. (1974). Response programming in simple and choice reactions. *Journal of Motor Behavior*, 6(4): 263-271. doi:10.1080/00222895.1974.10735002
- Kornblum, S., Hasbroucq, T., & Osman, A. (1990). Dimensional overlap: Cognitive basis for stimulus-response compatibility -- A model and taxonomy. *Psychological Review*, 97, 253-270. doi: 10.1037/0033-295X.97.2.253
- Kornhuber, H. H., & Deecke, L. (1965). Hirnpotentialänderungen bei Willkürbewegungen und Passiven Bewegungen des Menschen: Bereitschaftspotential und reafferente Potentiale. *Pflügers Archiv für die gesamte Physiologie des Menschen und der Tiere*, 248, 1-17
- Kristeva, R., Cheyne, W. Lang, G. Lindinger, G., & Deecke, L. (1990).

- Movement-related potentials accompanying unilateral and bilateral finger movements with different inertial loads. *Electroencephalography and Clinical Neurophysiology*, 75, 410-418. doi: 10.1016/0013-4694(90)90086-Y
- Kutas, M., & Donchin, E. (1977). The effect of handedness, of responding hand, and of response force on the contralateral dominance of the readiness potential. In J.E. Desmedt (Ed.), *Attention, Voluntary Contraction and Event-Related Cerebral Potential. Progress in Clinical Neurophysiology*, 1, Basel: Karger. Pp. 189-210.
- Kutas, M., McCarthy, G., & Donchin, E. (1977). Augmenting mental chronometry: The P300 as a measure of stimulus evaluation time. *Science*, 197(4305), 792-795. doi: 10.1126/science.887923
- Lee, K. M., Chang, K. H., & Roh, J. K. (1999). Subregions within the supplementary motor area activated at different stages of movement preparation and execution. *Neuroimage*, 9(1), 117-123. doi: 10.1006/nimg.1998.0393
- Leuthold, H., & Jentsch, I. (2011). Are temporal response features prepared in fixed order? Inferences from movement-related potentials. *Psychophysiology*, 48, 633-644. doi: 10.1111/j.1469-8986.2010.01126.x
- Leuthold, H., & Schröter, H. (2011). Motor programming of finger sequences of different complexity. *Biological Psychology*, 86, 57-64. doi: 10.1016/j.biopsycho.2010.10.007
- Leuthold, H., & Sommer, W. (1998). Postperceptual effects and P300 latency. *Psychophysiology*, 35(1), 34-46.

- Leuthold, H., Sommer, W., & Ulrich, R. (1996). Partial advance information and response preparation: Inferences from the lateralized readiness potential. *Journal of Experimental Psychology: General*, *125*(3), 307-323. doi: 10.1037/0096-3445.125.3.307
- Loveless, N. E., & Sanford, A. J. (1974). Effects of age on the contingent negative variation and preparatory set in a reaction-time task. *Journal of Gerontology*, *29*(1), 52-63. doi: 10.1093/geronj/29.1.52
- Low, M. D., & McSherry, J. W. (1968). Further observations of psychological factors involved in CNV genesis. *Electroencephalography and Clinical Neurophysiology*, *25*(3), 203-207. doi: 10.1016/0013-4694(68)90017-5
- Low, K. A., Miller, J., & Vierck, E. (2002). Response slowing in Parkinson's disease A psychophysiological analysis of premotor and motor processes. *Brain*, *125*(9), 1980-1994. doi: 10.1093/brain/awf206
- Luck, S.J. *An introduction to the event-related potential technique*. Cambridge, MA: MIT press, 2005.
- MacKay, W. A., & Bonnet, M. (1990). CNV, stretch reflex and reaction time correlates of preparation for movement direction and force. *Electroencephalography and Clinical Neurophysiology*, *76*, 47-62. doi: 10.1016/0013-4694(90)90057-Q
- Magliero, A., Bashore, T. R., Coles, M. G., & Donchin, E. (1984). On the dependence of P300 latency on stimulus evaluation processes. *Psychophysiology*, *21*(2), 171-186. doi: 10.1111/j.1469-8986.1984.tb00201.x

- Magnuson, C. E., Robin, D. A., & Wright, D. L. (2008). Motor programming when sequencing multiple elements of the same duration. *Journal of Motor Behavior*, *40*(6): 532-544. doi:10.3200/JMBR.40.6.532-544
- Masaki, H., Takasawa, N., & Yamazaki, K. (1997). The effect of parameter modification process during execution of a trigger pulling movement on readiness potential. *Japanese Journal of EEG and EMG*, *25*, 18-24.
- Masaki, H., Takasawa, N., & Yamazaki, K. (1998a). The effect of motor programming and the parameter-applying-processes on the readiness potential. *Japanese Journal of Physiological Psychology and Psychophysiology*, *16*, 85-91.
- Masaki, H., Takasawa, N., & Yamazaki, K. (1998b). Enhanced negative slope of the readiness potential preceding a target force production task. *Electroencephalography and Clinical Neurophysiology*, *108*, 390-397.
10.1016/S0168-5597(98)00019-7
- Masaki, H., Wild-Wall, N., Sangals, J., & Sommer, W. (2004). The functional locus of the lateralized readiness potential. *Psychophysiology*, *41*, 220-230. doi: 10.1111/j.1469-8986.2004.00150.x
- Matsumoto, E., Misaki, M., & Miyauchi, S. (2004). Neural mechanisms of spatial stimulus-response compatibility: The effect of crossed-hand position. *Experimental Brain Research*, *158*(1), 9-17. doi: 10.1007/s00221-004-1872-7
- McAdam, D. W. & Seales, D. M. (1969). Bereitschaftspotential enhancement with increased level of motivation. *Electroencephalography and Clinical*

Neurophysiology, 27, 73-75. doi: 10.1016/0013-4694(69)90111-4

McClelland, J. L. (1979). On the time relations of mental processes: An examination of systems of processes in cascade. *Psychological Review*, 86(4), 287-220. doi: 10.1037/0033-295X.86.4.287

Miller, J., Patterson, T., & Ulrich, R. (1998). A jackknife-based method for measuring LRP onset latency difference. *Psychophysiology*, 35, 99-115. doi:10.1111/1469-8986.3510099

Miller, J., Riehle, A., & Requin, J. (1992). Effects of preliminary perceptual output on neuronal activity of the primary motor cortex. *Journal of Experimental Psychology*, 18, 1121-1138. doi: 10.1037/0096-1523.18.4.1121

Mordkoff, J. T., & Gianaros, P. J. (2000). Detecting the onset of the lateralized readiness potential: A comparison of available methods and procedures. *Psychophysiology*, 37(3), 347-360. doi: 10.1111/1469-8986.3730347

Müller-Gethmann, H., Rinkenauer, G., Stahl, J., & Ulrich, R. (2000). Preparation of response force and movement direction: Onset effects on the lateralized readiness potential. *Psychophysiology*, 37(4): 507-514. doi: 10.1111/1469-8986.3740507

Müller-Gethmann, H., Ulrich, R., & Rinkenauer, G. (2003). Locus of the effect of temporal preparation: Evidence from the lateralized readiness potential. *Psychophysiology*, 40(4): 597-611. doi: 10.1111/1469-8986.00061

Nicoletti, R., Umiltà, C., & Ladavas, E. (1984). Compatibility due to the coding of the relative position of the effectors. *Acta Psychologica*, 57(2), 133-143. doi:

10.1016/0001-6918(84)90039-8

- Oldfield, R. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 97-113. doi: 10.1016/0028-3932(71)90067-4
- Osman, A., Moore, C. M., & Ulrich, R. (1995). Bisecting RT with lateralized readiness potentials: Precue effects of LRP onset. *Acta Psychologica*, *90*(1): 111-127. doi: 10.1016/0001-6918(95)00029-T
- Ragot, R. (1984). Perceptual and motor space representation: An event-related potential study. *Psychophysiology*, *21*(2), 159-170. doi: 10.1111/j.1469-8986.1984.tb00199.x
- Ray, W. J., Slobounov, S., Mordkoff, J., Johnston, J., & Simon, R. F. (2000). Rate of force development and the lateralized readiness potential. *Psychophysiology*, *37*(06), 757-765. doi: 10.1111/1469-8986.3760757
- Rohrbaugh, J. W., Syndulko, K., & Lindsley, D. B. (1976). Brain wave components of the contingent negative variation in humans. *Science*, *191*(4231), 1055-1057. doi: 10.1126/science.1251217
- Riggio, L., Gawryszewski, L. D., & Umiltà, C. (1986). What is crossed in crossed-hand effects? *Acta Psychologica*, *62*(1), 89-100. doi: 10.1016/0001-6918(86)90006-5
- Rosenbaum, D. A. (1980). Human movement initiation: Specification of arm, direction and extent. *Journal of Experimental Psychology: General*, *109*, 444-474. doi: 10.1037/0096-3445.109.4.444.
- Rosenbaum, D. A. (1983). The movement precuing technique: Assumptions, applications, and extensions. *Advances in psychology*, *12*, 231-274. doi:

10.1016/S0166-4115(08)61994-9

- Rosenbaum, D. A., Inhoff, A. W., & Gordon, A. M. (1984). Choosing between movement sequences: A hierarchical editor model. *Journal of Experimental Psychology: General*, *113*(3), 372-393. doi: 10.1037/0096-3445.113.3.372
- Rosenbaum, D. A. (1985). Motor programming: A review and scheduling theory. In H. Heuer, U. Kleinbeck, & K. -H. Schmidt (Eds.), *Motor behavior: Programming, control, and acquisition* (pp. 1-33). Berlin: Springer-Verlag.
doi:10.1007/978-3-642-69749-4_1
- Rosenbaum, D. A., Hindorff, V., & Munro, E. M. (1987). Scheduling and programming of rapid finger sequences: Tests and elaborations of the hierarchical editor model. *Journal of Experimental Psychology: Human Perception and Performance*, *13*(2), 193-203. doi: 10.1037/0096-1523.13.2.193
- Rosenbaum, D. A., Saltzman, E., & Kingman, A. (1984). Choosing between movement sequences. In S. Kornblum & J. Requin (Eds.), *Preparatory States and Processes*. New Jersey: Erlbaum. Pp. 119-134. doi: 10.1037/0096-3445.113.3.372
- Sanders, A. F. (1998). *Elements of human performance: Reaction processes and attention in human skill*. Mahwah, NJ: Erlbaum.
- Sanders, A. F. (1990). Issues and trends in the debate on discrete vs. continuous processing of information. *Acta Psychologica*, *74*, 1-45. doi: 10.1016/0001-6918(90)90004-Y
- Sanders, A. F. (1980). Some effects of instructed muscle tension on choice reaction time

- and movement time. *Attention and Performance*, 8, 59-74.
- Schmidt, R. A. (1975). A schema theory of discrete motor skill learning. *Psychological Review*, 82, 225-260. doi: 10.1037/h0076770
- Schmidt, R. A. (1982). More on motor programs. *Human motor behavior: An introduction*, 189-217.
- Schmidt, R. A. (1988). *Motor control and learning*. Illinois: Human Kinetics Publishers, Inc. Pp. 75-139, Pp. 227-266.
- Schmidt, R., & Lee, T. (2013). *Motor Learning and Performance, 5E With Web Study Guide: From Principles to Application*. (pp. 107-108). Human Kinetics.
- Schröter, H., & Leuthold, H. (2008). Effects of response sequence length on motor programming: A chronometric analysis. *Acta Psychologica*, 128(1), 186-196. doi: 10.1016/j.actpsy.2007.12.006
- Schröter, H., & Leuthold, H. (2009). Motor programming of rapid finger sequences: Inferences from movement-related brain potentials. *Psychophysiology*, 46, 388-401. doi: 10.1111/j.1469-8986.2008.00772.x
- Schwarzenau, P., Falkenstein, M., Hoormann, J., & Hohnsbein, J. (1998). A new method for the estimation of the onset of the lateralized readiness potential (LRP). *Behavior Research Methods, Instruments, and Computers*, 30(1), 110-117. doi: 10.3758/BF03209421
- Shaffer, L. H. (1982). Rhythm and timing in skill. *Psychological Review*, 89(2), 109. doi: 10.1037/0033-295X.89.2.109

Shea, C. H., & Wulf, G. (2005). Schema theory: A critical appraisal and reevaluation.

Journal of Motor Behavior, 37(2), 85-102. doi: 10.3200/JMBR.37.2.85-102

Shibasaki, H., Barrett, G., Halliday, E., & Halliday, A. M. (1980). Components of the movement-related cortical potential and their scalp topography.

Electroencephalography and Clinical Neurophysiology, 49, 213-226.

Shulman, H. G., & McConkie, A. (1973). S-R compatibility, response discriminability, and response codes in choice reaction time. *Journal of Experimental Psychology*,

98(2), 375-378. doi: 10.1016/0013-4694(80)90216-3

Simon, J. R., Hinrichs, J. V., & Craft, J. L. (1970). Auditory S-R compatibility: Reaction time as a function of ear-hand correspondence and ear-response-location

correspondence. *Journal of Experimental Psychology*, 86, 97-102. doi:

10.1037/h0029783

Smulders, F. T. Y., Kenemans, J. L., & Kok, A. (1996). Effects of task variables on measures of the mean onset latency of LRP depend on the scoring method.

Psychophysiology, 33, 194-205. doi: 10.1111/j.1469-8986.1996.tb02123.x

Smulders, F. T., Kok, A., Kenemans, J. L., & Bashore, T. R. (1995). The temporal selectivity of additive factor effects on the reaction process revealed in ERP

component latencies. *Acta Psychologica*, 90(1), 97-109. doi:

10.1016/0001-6918(95)00032-P

Sparks, D. L., & Mays, L. E. (1983). Role of the monkey superior colliculus in the

spatial localization of saccade targets. In A. Hein., & M. Jeannerod (Eds), *Spatially*

- oriented behavior* (pp. 63-85). New York: Springer. doi:
10.1007/978-1-4612-5488-1_4
- Spijkers, W. A. C. (1987). Programming of direction and velocity of an aiming movement: The effect of probability and response-specificity. *Acta Psychologica*, 65(3): 285-304. doi: 10.1016/0001-6918(87)90054-0
- Spijkers, W. A. C., & Walter, A. (1985). Response processing stages in choice reactions. *Acta Psychologica*, 58(2): 191-204. doi: 10.1016/0001-6918(85)90007-1
- Spijkers, W. A. C., & Steyvers, F. J. (1984). Specification of direction and duration during programming of discrete sliding movements. *Psychological Research*, 46, 59-71. doi: 10.1007/BF00308593
- Stanovich, K. E., & Pachella, R. G. (1977). Encoding, stimulus-response compatibility, and stages of processing. *Journal of Experimental Psychology: Human Perception and Performance*, 3(3), 411. doi: 10.1037/0096-1523.3.3.411
- Sternberg, S. (1969). The discovery of processing stages: Extensions of Donders' method. *Acta Psychologica*, 30, 276-315. doi: 10.1007/BF00308593
- Sternberg, S. (2013). The meaning of additive reaction-time effects: Some misconceptions. *Frontiers in Psychology*, 4, 1-3. doi: 10.3389/fpsyg.2013.00744
- Tanji, J. (2001). Sequential organization of multiple movements: Involvement of cortical motor areas. *Annual Review of Neuroscience*, 24(1), 631-651. doi:
10.1146/annurev.neuro.24.1.631
- Ulrich, R., Leuthold, H., & Sommer, W. (1998). Motor programming of response force

- and movement direction. *Psychophysiology*, 35, 721-728. doi:
10.1111/1469-8986.3560721
- Ulrich, R., & Miller, J. (2001). Using the jackknife-based scoring method for measuring LRP onset effects in factorial designs. *Psychophysiology*, 38, 816-827. doi:
10.1111/1469-8986.3850816
- Van Boxtel, G. H. M., & Brunia, C. H. M. (1994). Motor and non-motor components of the contingent negative variation. *International Journal of Psychophysiology*, 17, 269-279. doi: 10.1016/0167-8760(94)90069-8
- Van Boxtel, G. J., Van den Boogaart, B., & Brunia, C. H. (1993). The contingent negative variation in a choice reaction time task. *Journal of Psychophysiology*, 7(1), 11-23.
- Van Duren, L. L., & Sanders, A. F. (1988). On the robustness of the additive factors stage structure in blocked and mixed choice reaction designs. *Acta Psychologica*, 69(1): 83-94. doi:10.1016/0001-6918(88)90031-5
- van Galen, G. P., & Teulings, H. L. (1983). The independent monitoring of form and scale factors in handwriting. *Acta Psychologica*, 54(1), 9-22. doi:
10.1016/0001-6918(83)90020-3
- Vaughan Jr, H. G., Costa, L. D., & Ritter, W. (1968). Topography of the human motor potential. *Electroencephalography and Clinical Neurophysiology*, 25(1), 1-10. doi:
10.1016/0013-4694(68)90080-1
- Verleger, R. (1997). On the utility of P3 latency as an index of mental chronometry.

- Psychophysiology*, 34(2), 131-156. doi: 10.1111/j.1469-8986.1997.tb02125.x
- Verwey, W. B. (1994). *Mechanisms of skill in sequential motor behavior*. Doctoral Dissertation. Free University, Amsterdam, Netherlands
- Wadman, W. J., Denier van der Gon, J. J., Geuze, R. H. & Mol, C.R. (1979). Control of fast goal-directed arm movements. *Journal of Human Movement Studies*, 5, 3-17.
- Wallace, R. J. (1971). S-R compatibility and the idea of a response code. *Journal of Experimental Psychology*, 88, 354-360. doi: 10.1037/h0030892
- Wallace, R. J. (1972). Spatial SR compatibility effects involving kinesthetic cues. *Journal of Experimental Psychology*, 93(1), 163. doi: 10.1037/h0032462
- Wallace, S. A., & Wright, L. (1982). Distance and movement time effects on the timing of agonist and antagonist muscles: A test of the Impulse-Timing theory. *Journal of Motor Behavior*, 14, 341-352. doi: 10.1080/00222895.1982.10735284
- Walter, W., Cooper, R., Aldridge, V. J., McCallum, W. C., & Winter, A. L. (1964). Contingent negative variation: an electric sign of sensori-motor association and expectancy in the human brain. *Nature*, 203, 380-384. doi: 10.1038/203380a0
- Zelaznik, H. N., & Franz, E. (1990). Stimulus-response compatibility and the programming of motor activity: Pitfalls and possible new directions. *Advances in Psychology*, 65, 279-295. doi: 10.1016/S0166-4115(08)61227-3
- Zelaznik, H. N., & Hahn, R. (1985). Reaction-time methods in the study of motor programming: The precuing of hand, digit, and duration. *Journal of Motor Behavior*, 17(2): 190-218. doi:10.1080/00222895.1985.10735344