Timing control mechanism in rapid interception actions

（打撃動作におけるタイミング制御メカニズム）

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CHAPTER 1

BRIEF HISTORY OF THE STUDY

Successful hitting action in fastball sports, such as baseball, cricket, tennis, and table tennis, requires extremely high spatiotemporal accuracy under severe time constraints. In these sports, a ball reaches the hitting point in less than half a second and hitting action typically takes approximately 200 ms. Furthermore, because opponents attempt to maximize the spatial and temporal uncertainty, both ball speed and trajectory are highly unpredictable. Even in such severe conditions, professional players are able to hit a ball with a spatiotemporal accuracy of a few centimeters and milliseconds (Gray, 2002). Understanding how our central nervous system achieves such a high performance under these extraordinary circumstances could reveal a fundamental human trait of motor control that we are unaware of in our daily lives.

1.1. Control strategy of rapid interceptive actions

First, this thesis focuses on timing control in rapid interceptive actions, not spatial control. For half a century, research on the basic nature of interception has focused mainly on the development of the control theory, which could explain observed behavior and temporal accuracy. Two broad schemes have been proposed: the preprogrammed control model and the continuous control model (Tyldesley and Whiting, 1975; Tresilian, 2005; Brenner and Smeets, 2011).

(i) Preprogrammed control

The preprogrammed control model assumes that motor command is entirely preprogrammed and not influenced by exteroceptive sensory information after the motor pattern generator has begun to generate a descending command. In this model, timing control is governed by two components: determination of movement time (MT: movement duration) and initiation of the predetermined movement at the right moment. A schematic of the preprogrammed control is shown in Fig. 1.1. Perceptual transmission time (PT) is the time in which information in the retinal images is transmitted through the nervous system to the circuit that makes a motor command. Transmission time (TT) is the time in which a command is transmitted to the muscles and the muscles to begin contracting in response to the command. For successful preprogrammed control, the moment that TTC = MT + PT + TT, has to be accurately detected. In addition, initiation of the movement at the right moment (when TTC of target = predetermined MT) and execution of the movement in predetermined MT (MT_{prog}) are required. This kind of control produces a short, ballistic movement with a bell-shaped velocity profile.

(ii) Continuous control

On the other hand, continuous control proposes that interceptive movement is continuously updated through sensory information (Lee et al., 1983; Bootsma and Van Wieringen, 1990; Peper et al., 1994). Thus, the timing of movement onset is not critical for accuracy in this scheme. It is established that actions with a relatively slow and long duration movement (MT > 500 ms), such as catching a fly ball, are executed by continuous control (Montagne et al., 1999). However, several previous studies have provided evidence for online correction in rapid interceptive action (MT: 200-400 ms) (Bootsma and Van Wieringen, 1990; Donkelaar et al., 1992; Port et al., 1997; Brenner et al.,

1998).

Moreover, many previous studies have found that movement durations are consistently shorter with fast-moving targets than with slow-moving targets, the so-called velocity-coupling effect (Bairstow, 1987; Bootsma and Van Wieringen, 1990; Smeets and Brenner, 1995; Mason and Carnahan, 1999; Gray, 2002a; Tresilian and Lonergan, 2002; Tresilian et al., 2003; Caljouw et al., 2004). Some studies have concluded that this coupling is a result of online continuous control (Lee et al., 2001; Merchant and Georgopoulos, 2006) and a strategy to increase temporal accuracy in rapid interception (Tresilian and Lonergan, 2002; Tresilian et al., 2003).

Taken together, timing control in rapid interceptive action might be governed by both preprogrammed and continuous control. However, it is unclear to what extent an interpersonal variability exists in the control strategy if it results in higher temporal accuracy.

1.2. Time constraints from neurophysiological delay

(i) Visuomotor delay for online correction

Visuomotor delay (VMD) for online correction is described as the moment when target velocity or trajectory changes to the moment when the correction of ongoing movement profiles is detected. In psychological experiments, experts' VMD in fastball sports ranges from 150 to 250 ms, depending on the task and level of inertia that must be overcome (Le Runigo et al., 2005, 2010). Some previous studies have reported a shorter VMD that is less than 100 ms (Angel and Higgins, 1969; Lee et al., 1983; Bootsma and Van Wieringen, 1990). However, in the paradigm in these studies, error detection could occur before movement onset (i.e., premotor time). In contrast, in the experiment

conducted by Le Runigo et al. (2005, 2010), the kinematic change of a moving target occurred after participants' movement onset. Therefore, this extremely short VMD cannot be compared with the VMD reported in Le Runigo et al. (2005, 2010). Because swing duration is typically approximately 200 ms (Gray, 2002a), the efficacy of online correction in rapid interception has been thought to be marginal or impossible. However, in an actual game, an error for decision making of movement duration and onset could be detected and therefore online correction might contribute to temporal accuracy in rapid interception. This point will be argued in the first experiment of this thesis.

(ii) *Processing time for the decision of movement onset*

Motor command generation in rapid interceptive action is initiated by a visually perceived quantity (i.e., TTC_{tgt}: time-to-contact of moving target) reaching a critical value. This value is illustrated in Fig. 1.1 as PT + TT. This value has been reported to be about 150 ms (Marinovic et al., 2009). That is, MT + 150 ms + "time for determining MT" is thought to be an indispensable formula for accurate control of movement onset. Considering the above-mentioned severe time constraint in fastball sports, there does not seem to be enough time for the decision of movement onset. The question of how we overcome this difficulty will be argued in the second experiment of this thesis.

(iii) *Anticipatory skills in rapid interception*

Research on batting in cricket, baseball, or other striking sports indicates an advantage of anticipatory-information pickup in fastball sports as reviewed in Müller & Abernethy (2012). In cricket batting, the ball, which may travel up to 160 km/s, can deviate through the air and change its trajectory after it hits the ground. Highly skilled cricket batsmen extract advance cue information from the bowler's arm movements before the ball is released and these

differences in information pickup are found not only between novice and skilled cricketers, but also between skilled and elite cricketers (Müller & Abernethy, 2012). This benefit could pose a risk of incorrect initiation of movement because the anticipatory information is not always exact. Thus, an ability to inhibit ongoing swings (even before the initiation of movement) or to correct the swing speed and trajectory might be crucial for successful performance.

(iv) Inhibitory control

For over 20 years, the ability to inhibit a planned motor action has been investigated. Studies have found that the probability of successful inhibition of the motor action increases with a decrease in the interval between the go-and-stop signals. These behavioral data have been modeled as a race between two independent processes that respond to go signals and stop signals (Logan et al., 1984; Boucher et al., 2007; Schmidt et al., 2013). This race model takes into account only two motor outcomes (complete inhibition and full response) because previous studies have used binary button press tasks. However, it has been demonstrated that there are two other inhibitory responses: partial response, which has significantly lower electromyographic (EMG) activity than a full response, and interrupted response, which has the same initial activity as a full response but deviates suddenly from the full response profile (Kudo and Ohtsuki, 1998; McGarry and Franks, 2003). Gray (2009) reported that these flexible inhibitory responses have been observed in baseball batting depending on the timing of stop signals. In this study, the baseball batting simulation was the same as in the previous experiment (Gray, 2002a), while the timing of the trajectory deviation and the launch angle of the pitched ball were different. Participants were instructed to swing only in the "strike" zone and to withhold the swing when the ball crossed the "ball"

zone. The two most common responses were full swing and complete inhibitions, but 20% of the total swings were successful partial responses and interrupted responses of the swing action after the swing was initiated. Gray also reported that the expert athlete has a higher sensitivity in making the ball/strike decision than less experienced batters (Gray, 2010). It seems that this flexible inhibition of the ongoing swing reduces the anticipation cost and enables the utilization of provisional preprogrammed control at the start of the swing. The utilization of inhibitory control in the timing of rapid interception will be investigated in the second experiment in this thesis. More detailed neurophysiological backdrop will also be introduced in this section.
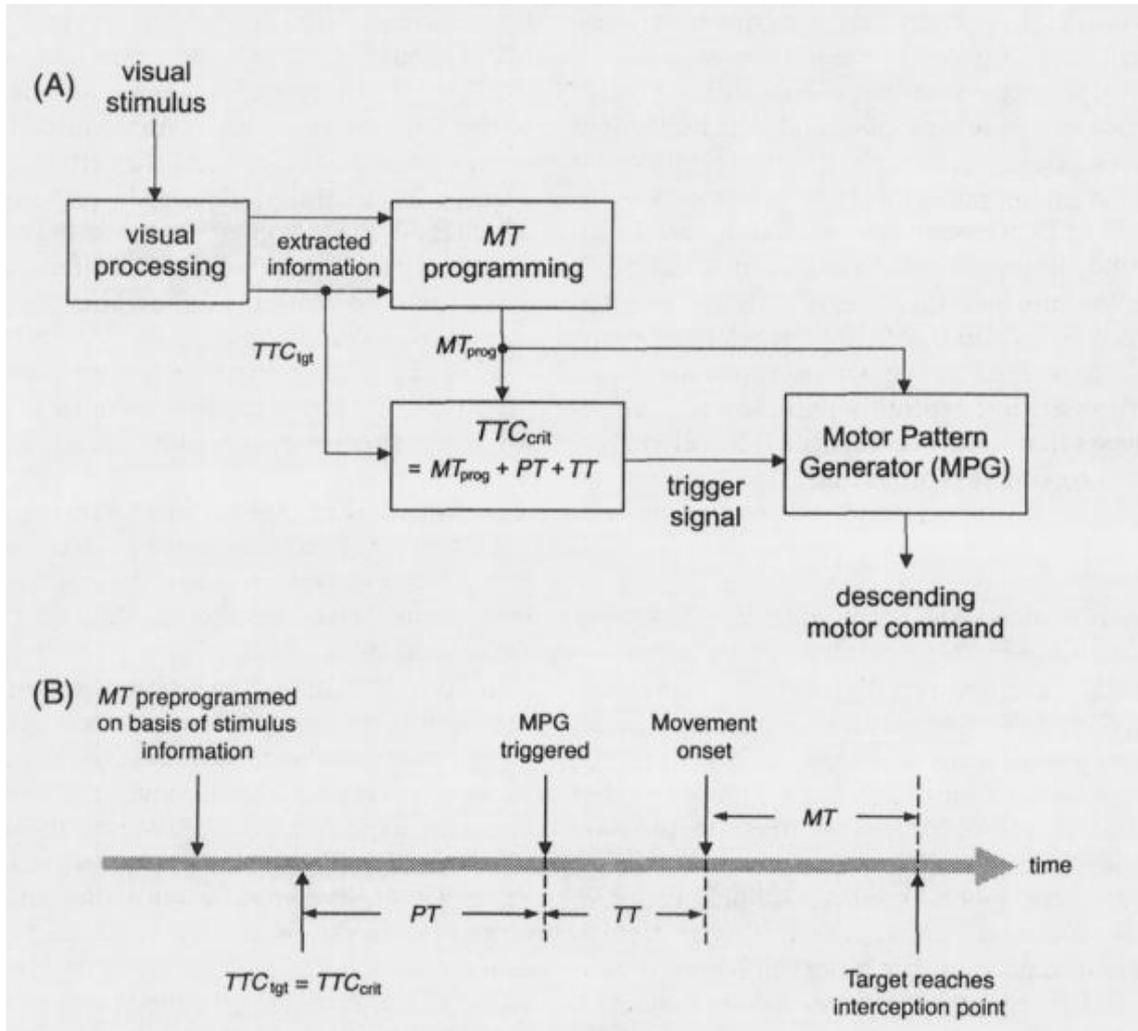
Fig. 1.1 (A) Block diagram of the preprogramming control and (B) temporal sequence of events in this scheme. PT (perceptual transmission time) is the time in which information in the retinal images is transmitted through the nervous system to the circuit that make a motor command. TT (transmission time) is the time in which a command is transmitted to the muscles and the muscles to begin contracting in response to the command. PT + TT is defined as the visuomotor delay for movement onset. Modified from Tresilian (2005).

CHAPTER 2

PURPOSE AND OUTLINE OF THIS THESIS

As described in Chapter 1.1, two control strategies could be used in timing control of rapid interceptive action. As both strategies have a benefit to increase temporal accuracy; therefore it is unclear how these two control strategies are employed in rapid interceptive action. It is also unclear whether there is an interpersonal variability in the use of control strategies and the relationship between control strategy and temporal accuracy. In addition, as described in Chapter 1.2, there is a debate about the efficacy of online correction in rapid interceptive action because the neurophysiological delay is relative long (150–250 ms) as opposed to a short and rapid (200–300 ms) movement. Finally, from a conventional framework of serial-information processing (Schmidt and Lee, 2011), there does not seem to be enough time for movement-onset decision making.

Overall, there are three main topics in this thesis: (1) Interpersonal variability in timing control strategy and temporal accuracy, (2) efficacy of online correction in rapid interception, and (3) the mechanism by which severe time constraints are overcome in the decision making of movement-initiation timing.

Study 1 (Chapter 3): Interpersonal variability in timing strategy and temporal accuracy in rapid interception tasks with variable time-to-contact

I required participants to compensate a 130 ms of difference in time-to-contact (TTC) by changing their movement onset and/or movement duration in a manual interception task. In the first experiment, I imposed a relatively easy time constraint (Slow: 670 ms and Medium: 540 ms). In the second experiment, I imposed a more severe time constraint (Medium: 540 ms and Fast: 410 ms).

In the third experiment, presented target speed was the same in every trial in each block (Single-speed condition) and investigated the effect of speed/TTC discrimination on the control strategy and temporal accuracy.

Study 2 (Chapter 4): Subthreshold excitability modulation of the subcortical motor circuit circumvents time constraint in the timing of movement initiation

Participants conducted almost the same task as in Experiment 1. In the single-speed (SS) condition, the time-to-contact (TTC) was 800 ms (Slow) in every trial. In the paired-speed (PS) condition, TTC was 800 ms (Slow) and 500 ms (Fast). In both conditions, a very loud startling acoustic stimulation (SAS) was presented in one out of ten trials 150 ms after target release. We used this startle technique to probe the excitability of the subcortical motor circuit including the basal ganglia and thalamus. When participants were intending to initiate some prepared actions and a SAS was presented just before initiation, it could evoke the preprogrammed motor command (StartReact). Analyzing the StartReact incidence, we can assess the activity level of the subcortical motor circuit. The only difference between the two conditions was the potentially anticipated fast-speed target. I hypothesized that a pre-activation of the motor circuit would occur only in the paired-speed condition for the timing of the fast speed target. This pre-activation below the threshold level should decrease the time taken to initiate the movement under a severe time constraint. I also expect that the experimental data will depict an involvement of inhibitory control to prevent false movement initiation at incorrect fast timing.

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CHAPTER 3

INTERPERSONAL VARIABILITY IN TIMING STRATEGY AND

TEMPORAL ACCURACY IN RAPID INTERCEPTION TASK

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3.1. Introduction

In rapid interceptive actions such as hitting a baseball, cricket ball, or tennis ball, we can achieve a high performance (Regan, 1992) in spite of extremely severe time constraints that are close to the limit of human visuomotor capacity. Because the time from the ball release and the moment of contact with the bat (time-to-contact: TTC) in baseball or cricket are very short and quite variable (usually 400–600 ms), batters have a limited time period in which to compensate for the TTC difference between faster and slower balls. To compensate for the TTC difference, we can decide when to start and how fast to move (i.e., time- and state-dependent control (Diedrichsen et al., 2007)). As a result, movement onset and/or movement duration are varied for compensation. There has been a longstanding debate about how these two variables are determined in rapid interceptive actions (Tresilian, 2005; Merchant and Georgopoulos, 2006; Zago et al., 2009).

In an actual sports game, there is a constraint on movement velocity because batters attempt to hit the ball as fast as possible. Therefore controlling the movement onset with a fixed minimum-movement duration (time-dependent control) might be an ideal strategy in an actual game. This so-called operational timing hypothesis was proposed by Tyldesley & Whiting (1975) as a control strategy of expert athletes who have learned to stabilize a particular motor program over their many years of training. By setting the movement duration constant in advance of seeing the moving target (i.e., *motor set* based on advance information), only the moment of initiating the movement has to be controlled.

Actually, this kind of time-dependent control has been observed in many rapid interceptive sports (Hubbard and Seng, 1954; Tyldesley and Whiting, 1975; Franks et al., 1985), psychophysical studies on interception (Lacquaniti

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and Maioli, 1989; Tresilian and Plooy, 2006; Marinovic et al., 2009), and reflex gain tuning (Wang et al., 2001; Kimura and Gomi, 2009). However, when there is not enough time to discriminate the TTC/speed of a moving target under a severe time constraint, it becomes difficult to accurately modulate the movement onset with a fixed-movement duration. Moreover, there would be a negative aspect such that the shorter the movement duration (e.g., < 200 ms), the less time for a feedback-based error correction due to a relatively long visuomotor delay (Le Runigo et al., 2005, 2010). Therefore it is unclear whether mainly controlling the movement onset really maximizes temporal accuracy.

On the other hand, many previous studies have reported that movement durations are consistently shorter for fast-moving targets than for slow-moving targets, the so-called velocity-coupling effect (Bairstow, 1987; Bootsma and Van Wieringen, 1990; Smeets and Brenner, 1995; Mason and Carnahan, 1999; Gray, 2002a; Tresilian and Lonergan, 2002; Tresilian et al., 2003; Caljouw et al., 2004). This effect has been observed even when participants are instructed to hit a moving target as quickly as possible (Smeets and Brenner, 1995). In this case, movement duration would be more modulated by the target speed. Intereception of a faster-moving target requires more temporal accuracy and it has been found that when the required temporal precision is greater, movment speed increases and movement duration decreases (Tresilian and Lonergan, 2002; Tresilian et al., 2003). Therefore, it has been suggested that the speed-coupling effect is a strategy to increase temporal accuracy.

Taken together, both control strategies mentioned above have a factor that increases temporal accuracy. Hence, there could be an interpersonal variability in the weighting between movement onset and duration to be controlled, which has been partly found in a previous study (Port, Lee,

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Dassonville, & Georgopoulos, 1997). However, this study did not report on temporal accuracy, thus the relationship between control strategy and task performance remains unknown.

   In the current study, we conducted three experiments to investigate the above issues. In the first experiment, we investigated to what extent a different mode exists in control strategy in terms of movement onset and movement duration for the compensation of TTC. In the second experiment, we imposed a more severe time constraint and examined the constraint impact on control strategies. Furthermore, the relationship between the control strategies and temporal accuracy was analyzed. Finally, in the third experiment, we examined the effect of a requirement of speed/TTC discrimination on control strategy and temporal accuracy in which the TTC of a moving target was not varied between trials and participants do not need to discriminate the speed/TTC.

3.2. Methods

(i) Participants

Twenty-six young males participated in the experiment (mean age: 20 years; range: 18–24). None had fastball-sports experience (e.g., baseball, cricket, or tennis) on a competitive level. We recruited novices because a person with fastball-sports experience may have a biased and implicit preference for control strategy due to the constraint on movement velocity in actual games. The participants were all right handed and had normal or corrected-to-normal vision and gave informed consent prior to participation in the study. Ethical approval for this study was granted by the Ethical Committee of The University of Tokyo (approval number: 216).

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(ii) Task

The experimental task was to intercept a virtual moving target (ball) with a virtual bar (bat) projected onto a computer monitor. Participants controlled the bar by the extension and flexion of their left elbow joint using a manipulandum (Fig. 3.1A). After participants set the bar to the initial position and waited 1000 ms, an auditory ready cue was provided. After an interval of 500 ms, the target was then released downward at a constant speed. Since the interval was fixed, participants were able to anticipate the timing of the ball release, which mimicked a real batting situation in which batters can anticipate the approximate timing of the ball release based on a pitching motion. Therefore participants could use the anticipatory skills in this task as described in chapter 1.2. Participants were instructed to fully extend their elbow joint to complete their swing and not to stop the bat. The speed of the moving target varied between trials and participants had to adjust their interceptive timing by changing their movement onset and/or duration.

(iii) Apparatus

Each participant sat on a chair and placed his chin on a chin rest to stabilize his face position. Participants' eyes were at a horizontal distance of 1.0 m from a computer monitor set in portrait orientation (23.6 inch, 1920 × 1080 pixels, and a 120 Hz refresh frequency). The length of the bat was 5.4 cm (200 pixels) and the axis of the bat rotation was fixed at a vertical distance of 27.2 cm (1000 pixels) from the ball-release point. Participants rested their left forearms on a linear plate of the manipulandum and gripped a metallic rod attached to the manipulandum. Rotation of the manipulandum, indicating the elbow-joint angle, was measured by a potentiometer and converted to the same degree of rotation of the virtual bat. The virtual bat angle was rotated counter clockwise 25 degrees with respect to the actual angle of

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manipulandum. The initial bat position was set to -65 degrees from the horizontal line (desired hit position). Participants were instructed to intercept the ball at the desired hit position.

(iv) Visual stimuli

The virtual ball was black and the diameter was 10.9 mm (40 pixels; corresponding to 0.62° viewing angle). There were three different ball speeds for which the ideal time-to-contact (TTC) was 410 ms (Fast), 540 ms (Medium), and 670 ms (Slow). The TTC for the fastball was comparable to that of a 145 km/h (92 mph) fastball in baseball and the slow ball corresponded to a 92 km/h (57 mph) breaking ball. Note that all types of pitches were at constant speed. The visual stimuli were controlled using a customized program written in LabVIEW 2010 software (National Instruments, Austin, TX, USA).

(v) Experimental design and procedure

In the first main experiment, the combination of TTC was set at 670 ms (Slow) and 540 ms (Medium). The proportion of the two ball speeds was set at 50% and the order of the speeds was pseudo-randomized. In every trial, participants were provided with two kinds of feedback about spatial error. One was visual feedback, provided by stopping the update of the bat angle and the ball position at the time of contact. The other was the value of the bat angle at the moment of contact. We chose these two spatial errors because in a preliminary experiment, the combination of visual and numerical feedback of spatial error was more useful than either of the two types of feedback alone or the temporal error. Participants performed four sets of 24 trials (96 trials in total) for each of the two conditions. A 1 min rest was given between every set. As the control strategies of each participant became stable in the first or second set, the first half of the four sets was regarded as a practice session

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and the latter half was analyzed.

We conducted the second experiment to investigate the impact of a severe time constraint on the control strategies. We set the combination of TTC as 540 ms (Medium) and 410 ms (Fast). Other settings were the same as the first experiment.

The third experiment was conducted to evaluate the required effect of discriminating the TTC/speed of a moving target. We employed a single-speed (SS) condition (Slow, Medium, or Fast) in which the speed of the ball was the same in every trial for each block and participants performed three blocks of each speed. Participants performed 12 trials in one set and conducted 4 sets (48 trials in total) in each speed condition.

Prior to the experimental sessions, we measured participants' simple reaction time and minimum movement duration. These measurements were indices of each participant's visuomotor processing time and maximum motor capacity. In the simple reaction time task, the ball was released without the auditory cue and participants attempted to start their movement as soon as possible. To measure the minimum movement duration, participants performed the elbow extension at their maximum speed. Participants performed 12 trials in one set and conducted 2 sets in total for each task.

(vi) Recording system

The elbow-angle data were measured using an analogue potentiometer. All data were digitally sampled at 1000 Hz (USB-6259, National Instruments) using a customized program written by LabVIEW 2010 software (National Instruments). Electromyography (EMG) signals were acquired using a double differential surface electrode (DE-3.1, Delsys, Boston, MA, USA) with an analogue bandpass filter (20–450 Hz) from the triceps brachii and biceps brachii. The EMG signals were amplified (gain: 1000) using an EMG amplifier (BAGNOLI-8, Delsys).

(vii) Analyses of control strategy

The data were analyzed offline using MATLAB (Mathworks, Natick, MA, USA) software and JMP10 (SAS Institute, Cary, NC, USA). The elbow-angle data were digitally low-pass filtered with a fourth-order, zero-phase-lag Butterworth filter at a cut-off frequency of 15 Hz.

In the paired-speed (PS) conditions, participants had to compensate for 130 ms (i.e., 670–540 in the slow/medium [S/M] and 540–410 in the medium/fast [M/F] condition) in the TTC difference between the faster and slower ball by changing the movement onset and/or movement initiation timing. To analyze the interpersonal difference in control strategies in the PS condition, we calculated movement onset and movement duration for every trial from the bat-angle data. Movement onset was defined as the time between target release and the moment at which the angular velocity of the bat rotation reached 10 degrees/s with the following 50 ms exceeding the threshold. Movement duration was defined as the time between movement onset and the moment at which the bat angle reached the desired hit point. We then calculated the mean differences in movement onset and duration (delta onset and delta duration) between the faster and slower target speeds. When the delta onset did not become a normal distribution, we divided our participants based on the delta onset. Those who mainly changed their movement duration were regarded as the "duration control group" and those who mainly changed their movement onset were regarded as the "onset control group"; temporal accuracy was compared between these two groups. When the delta onset became a normal distribution, we did not divide the participants and calculated a Pearson product-moment correlation coefficient between the delta onset and the temporal accuracy mentioned in the next section. In the single-speed (SS) condition, we conducted the same analysis as with the paired-speed (PS) condition and investigated the relationship between the

control strategy and temporal accuracy.

(viii) Analyses of task performance

To evaluate the task performance of the two groups, mean constant error (CE), variable error (VE) and total variability (TV) were analyzed as functions of error direction, variability, and overall accuracy in both the paired-speed (PS) and single-speed (SS) conditions. The CE represents the difference between the time at which the center of the ball reaches the desired hit point and the time at which the bat crosses the desired hit point (i.e., a negative value indicates a delayed contact and a positive value means an early contact). The VE is the standard deviation of the CE. The TV was computed as:

$$TV = \sqrt{CE^2 + VE^2}.$$

(ix) Simple reaction time and minimum movement duration

We calculated the simple reaction time and minimum movement duration to assess factors of interpersonal variability in the control strategy. Simple reaction time was defined as the time between target release and movement onset in the simple reaction-time task. Minimum movement duration was defined as the time between the movement onset and the moment at which the bat angle reached the desired hit point under maximum effort.

(x) EMG analysis for online correction latency

Because the difference in the control strategy was reflected in the EMG activity of the extensor (triceps brachii) but not the flexor muscle (biceps brachii), we analyzed only the extensor EMG data. To assess the processing time for the discrimination of target speed, we calculated the moment at which the averaged EMG amplitude deviated between faster- and slower-speed trials. We defined this value as an index of visuomotor delay. To

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guide this measure, we analyzed the moment at which a significant difference in the amplitudes was detected for at least 15 ms successively using a t-test ($p < 0.05$).

Moreover, to investigate the detailed mechanism of online correction in the rapid interception task, we calculated the latency of corrective EMG activity in Group 1. We first detected EMG onset in each trial using an algorithm that detected the time point at which EMG activity increased to more than 3 standard deviations (SD) above baseline (with a mean of 100 ms of EMG activity before target release). Then, we subtracted the mean EMG onset from the visuomotor delay.

(xi) Statistics

The three kinds of errors as well as simple reaction time and minimum movement duration were compared between the two groups using the Welch's t-test. The significance level was set at 0.05. For each variable, the effect size (Cohen's d, using a pooled standard deviation) was calculated to determine the strength of the difference between each condition. In the single-speed (SS) condition, we used a two-way repeated measures ANOVA with control strategy and target-speed factors to assess the susceptibility of the velocity-coupling effect.

3.3. Results

(i) Interpersonal variability in control strategies

In the first experiment, interpersonal variability in the control strategies was found with regard to the movement onset and duration. Some participants, among them participant 1 in Fig. 3.2B (delta onset: -16.2 ms, delta duration:

114.0 ms), started movements at the same approximate moment and exhibited different velocity profiles between target speeds. In contrast, other participants, such as participant 5 in Fig. 3.2C (delta onset: 98.7 ms, delta duration: 8.1 ms), consistently changed the moment of movement onset according to the target speeds with almost the same bell-shaped velocity profiles. Our participants could be separated into two groups (as shown in Fig. 3.2A) because the distribution of delta onset became bimodal, not normal (Shapiro-Wilk normality test: $W = 0.87$, $p < 0.001$). The difference in the control strategies also reflected other kinematic characteristic such as peak angular velocity and angular velocity at contact as shown in Table 3.1. Therefore, we divided our participants into Group 1 (duration control strategy group) and Group 2 (onset control strategy group). The number of participants and their mean, standard deviation (SD), and range of delta onset were as follows: Group 1: n = 15, delta onset: 7.96 ± 16.3 (-16.5–41.4) ms; Group 2: n = 11, 93.9 ± 10.8 (81.6–111.1) ms.

The movement onset (Table 3.1) of Group 1 (slow: 267 ms, medium: 259 ms) in the first experiment was nearly equal to the simple reaction time (253 ms). This result indicates a use of anticipatory movement onset before speed/TTC discrimination. When the speed was then slower than anticipated, movement velocity would have been adjusted in an ongoing fashion. The asymmetric non-bell-shaped velocity profiles shown in Fig. 3.2 support this speculation.

(ii) *Impact of a severe time constraint on control strategies*

In the second experiment, we imposed a more severe time constraint (410 ms and 540 ms). As a result, a shift of onset control strategy to duration control strategy was observed. Most participants in Group 1 in the first experiment largely maintained their control strategy in the second experiment (e.g., participant 1 (delta onset: 19.9 ms, delta duration: 86.1 ms) as shown in Fig.

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3.3B). On the other hand, many participants in Group 2 could not maintain their control strategy probably due to the severe time constraint in the second experiment (e.g., participant 5 (delta onset: 43.8 ms, delta duration: 73.8 ms) as shown in Fig. 3.3C). Delta onset of Group 1 in the second experiment was not significantly different from the first experiment (delta onset: 11.7 ± 25.3 (-39.5–52.8) ms, paired t-test: p = 0.58, t = 0.57). On the other hand, delta onset of Group 2 in the second experiment was significantly smaller than in the first experiment (delta onset: 55.0 ± 27.8 (-5.0–90.2) ms, paired t-test: p < 0.001, t = -7.0). Overall, the delta onset (Fig. 3.3A) became a normal distribution (Shapiro-Wilk normality test: W = 0.98, p = 0.80).

(iii) Relationship between temporal accuracy and control strategies

In the first experiment, we divided our participants into two groups according to the control strategies and therefore we compared the temporal acccuracy between these groups (Fig. 3.4A). Overall, Group 2 (onset control strategy group) outperformed Group 1 (duration control strategy group). The constant error (CE) in Group 2 was significantly smaller than in Group 1 for the medium speed ($t = 4.33$, $p < 0.001$, $d = 1.71$). The variable error (VE) in Group 2 was significantly smaller than in Group 1 for the slow speed ($t = 4.06$, $p < 0.001$, $d = 1.43$). The total variability (TV) in Group 2 was smaller than in Group 1 for both speeds in the S/M condition (Slow: $t = 4.92$, $p < 0.001$, $d = 1.71$; Medium: $t = 3.87$, $p < 0.001$, $d = 1.41$). No other significant differences were found in either condition (CE of slow speed: $t = 1.99$, $p = 0.059$, $d = 0.71$, VE of medium speed: $t = 1.44$, $p = 0.16$, $d = 0.52$).

In the second experiment, the control strategies did not distinctively polarize, therefore we analyzed the correlation between delta onset and temporal accuracy. As a result as shown in Fig. 3.4B, all temporal accuracies were significantly correlated with delta onset. The CE showed negative

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correlation for medium speed ($r = $ -0.72, $p < 0.001$) and positive correlation for fast speed ($r = 0.43$, $p = 0.029$). The VE showed negative correlation for both speeds (medium: $r = $ -0.58, $p = 0.0020$, fast: $r = $ -0.59, $p = 0.0015$). The TV showed negative correlation for both speeds (medium: $r = $ -0.72, $p < 0.001$, fast: $r = $ -0.50, $p = 0.0085$).

(iv) Effect of speed/TTC discrimination

In the third experiment (Single-speed condition), the difference in susceptibility to the speed-coupling effect was found only in Group 1 participants. A two-way repeated-measures ANOVA for movement duration (Table 1) showed a significant main effect of Group [$F(1,24) = 16.2$, $p < 0.001$] and of Speed [$F(2,48) = 18.0$, $p < 0.001$], as well as a significant interaction [$F(2,48) = 5.40$, $p < 0.01$]. Post-hoc analysis showed that movement duration of Group1 in fast speed was shorter than of medium speed ($p = 0.012$) and that of medium speed was shorter than that of slow speed ($p = 0.001$). This result indicates that participants in Group 2 tended to mainly modulate their movement onset (S-M: range 93.8-146.9, mean ± SD 127.4 ± 15.5, M-F: range 60.3-145.8, mean ± SD 110.0 ± 28.4), whereas participants in Group 1 employed a wide range of combinations of movement onset and duration (S-M: range -21.2-171.5, mean ± SD 96.4 ± 49.4, M-F: range 17.1-110.6, mean ± SD 74.1 ± 26.9).

Although we observed such a difference, the delta onset in the SS condition (Fig. 3.5) became a normal distribution (Shapiro-Wilk normality test: $W > 0.95$, $p > 0.29$). Thus, we did not compare the temporal accuracy between the two groups and analyzed a correlation between delta onset and temporal accuracy. Interestingly, in contrast to the results in the first and second experiments, temporal accuracies were only partially correlated with delta onset. The delta onset (S-M) showed significant negative correlation with CE in medium speed

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(r = -0.56, p = 0.003) and the delta onset (M-F) exhibited significant positive correlation with CE in fast speed (r = 0.52, p = 0.007). No other significant differences were found in either condition (t = 0.071 – 1.67, p = 0.11 – 0.94, d = 0.03 – 0.65).

(v) Simple reaction time and minimum movement duration

A small but significant difference in the simple reaction time and minimum movement duration between Groups 1 and 2 revealed that participants in Group 2 had higher visuomotor processing and motor abilities than participants in Group 1. The simple reaction time in Group 1 was significantly longer than in Group 2 (253 ± 16.2 vs. 236 ± 18.4 ms, t =2.56, p = 0.019, d = 1.04) and the minimum movement duration in Group 1 was significantly longer than in Group 2 (193 ± 16.5 vs. 169 ± 15.0 ms, t = 3.89, p < 0.001, d = 1.52).

(vi) EMG analysis

Fig. 3.7A and Fig. 3.7B show examples of the ensemble average of rectified extensor EMG activity in Group 1 (Fig. 7A) and Group 2 (Fig. 7B). The visuomotor delays indicated by the black arrow in Fig. 7 do not differ between the two groups in both PS conditions (PS S/M: Group 1: 246.2 ± 16.7 ms, Group 2; 267.2 ± 29.7 ms, t = 1.83, p = 0.084, d = 0.81, PS M/F: Group 1: 210.9 ± 20.8 ms, Group 2: 198.2 ± 20.1 ms, t = 1.35, p = 0.19, d = 0.61). In the PS S/M condition, the average EMG onset in Group 1 for the slow speed and the medium speed were 172.1 ± 76.6 ms and 174.2 ± 56.8 ms (Fig. 7C). In the PS M/F condition, the mean value of EMG onset in Group 1 for the medium ball and the fast ball were 142.1 ± 69.2 ms and 135.5 ± 52.7 ms, indicating that online correction occurred in the EMG activity around 70 ms after EMG onset.

3.4. Discussion

The main purpose of this study was to investigate interpersonal variability in control strategy and task performance in a rapid interception task in which multiple TTCs were anticipated. The main finding was that our participants were divided into two groups: the participants in Group 1 mainly changed their movement duration, and the participants in Group 2 mainly modulated their movement onset to compensate for the 130 ms of difference in TTC (Fig. 3.2). Additionally, we imposed more a severe time constraint and assessed the effect of the constraint on control strategy. We then found that under the constraint, the control strategy of Group 2 shifted to that of Group 1, although Group 1 largely maintained their control strategy (Fig. 3.3). Furthermore, the strategy that mainly modulated movement onset resulted in higher temporal accuracy in both the first and second experiments (Fig. 3.4).

(i) Difference in control strategy

Because minimum movement duration was about 190 ms in our experimental task, there was about 350 ms before movement onset based on the faster target speed in the first experiement (TTC was 670 and 540 ms). It has been reported that visual events that trigger a motor command occur at about 150 ms before movement onset (Marinovic et al., 2009); therefore, the time available for movement decision making was about 200 ms.

In spite of the relatively easy time constraint, the interpersonal variability in control strategies were observed in the first experiment. This result differs from that of Port et al. (1997), who reported that for short TTC (i.e., 500 and 800 ms), participants produced a single movement with symmetrical and bell-shaped velocity profiles. On the other hand, for longer TTC (i.e., 1100–2000 ms), participants could use either strategy, which is a similar result to

that of the current study. In our task, we provided ready-cue 500 ms before the target release, whereas Port et al. (1997) did not use this kind of ready cue. Thus, our participants were able to anticipate the timing of the target release, which is similar to the way baseball hitters or cricket batters anticipate the timing of the ball release by observing the pitching motion (de Lussanet et al., 2001; Gray, 2002b; Müller and Abernethy, 2012). Actually, the movement onset (Table 3.1) of Group 1 (slow: 267 ms, medium: 259 ms) in the first experiment was nearly equal to the simple reaction time (253 ms), which strongly indicates that participants determined the movement onset before the discrimination of speed/TTC of the target. Probably, most of the participants in Group 1 (as shown in Fig. 3.2B and Fig. 3.3B) anticipatorily started their movement for the timing of a faster-moving target and adjusted for a slower-moving target in an ongoing fashion (Donkelaar et al., 1992; Lee et al., 2001).

So why did the interpersonal variability exist? It has been suggested that successful operational timing of interception requires the following: (1) an accurate estimation of TTC and detection of the moment at which the motor command is triggered, (2) initiation of the movement at the right moment, and (3) execution of the movement in the predetermined duration (Tresilian, 2005). It is plausible to assume that those with a high capacity in these factors tended to modulate movement onset and vice versa.

First, the difference in the sum of minimal movement duration and simple reaction time (Group1: 446 ms vs. G2: 405 ms) provides a indication of the existence of such interpersonal variability. This result indicates that participants in Group 2 potentially had extra time (about 40 ms) for decision making, which would have enhaced the accuracy in the estimation of TTC and/or the detection of the moment of movement onset. Secondly, in a single-speed condition (i.e., no requirement of speed/TTC discrimination),

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there was no significant difference in the standard deviation of movement onset between the two groups, which suggests that participants in the two groups had an almost identical capacity in the second and third factors mentioned above. Therefore, we assume that the difference in accuracy for the onset control arose from the precision in discrimination and estimation of the speed/TTC of moving target.

In the second experiment, we imposed a more severe time constraint, in which the sum of the minimal movement duration and simple reaction time exceeded or was nearly equal to the shortest (410 ms) TTC. Therefore, for most of our participants, the decision-making time would be insufficient to discriminate speed/TTC and determine movement onset and duration. This constraint produced a strategy shift in Group 2 participants toward that of Group 1 in the second experiment (as shown in Fig. 3.2 and Fig. 3.3). On the other hand, participants in Group 1 largely maintained their control strategies. Taken together with the results from the first and second experiments, we assume that when the estimation of speed/TTC was inaccurate or the time for the estimation was insufficient, duration control strategy was mainly used.

(ii) Temporal accuracy and control strategies

Both onset control and duration control have been thought of as strategies to increase temporal accuracy in rapid interceptive action (Tresilian and Lonergan, 2002; Tresilian et al., 2003; Merchant and Georgopoulos, 2006). In the current study, modulating movement onset rather than movement duration resulted in higer temporal accuracy.

The correlation between the weight for onset control and temporal accuracy was not as notable in the single-speed condition. Taken together with these results, it is plausible to suggest that the process of speed/TTC discrimination

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causes the difference in temporal accuracy between the two control strategies. In a rapid interceptive action, the efficacy of feedback-based online correction is probably marginal because of a relatively long visuomotor delay for online correction (e.g., 162–221 ms (Le Runigo et al., 2005)). Therefore, it might be advantageous for temporal accuracy to depend on the control of movement onset with fixed and short ballistic movements in rapid interceptive actions.

(iii) Efficacy of online correction

The difference in task performance did not mean that online correction in the rapid interceptive task was ineffective. In fact, the corrective response occurred around 70 ms after the initial EMG onset of agonist activity in Group 1 participants (Fig. 3.7). This fast corrective response seems to be achieved by detecting a timing error and producing a corrective motor command before movement initiation. We believe that the underlying mechanism of the error detection before movement onset is the use of non-sensory feedback loops (see Desmurget & Grafton, 2000; Sabes, 2000 for a review) in which the consequence of motor output is estimated on the basis of an efference copy and compared with the future location of a moving target estimated on the basis of actual visual information. The efficacy of the non-sensory feedback loops has been reported in several psychophysical studies by Sonderen et al. (1989) and Cooke & Diggles (1984), in which correction of hand trajectory was observed within 20–40 ms after the initial movement onset in a double-step pointing task.

Finally, these findings from the current study have important practical implications for enhancing the timing accuracy in rapid interceptive actions such as hitting in cricket or baseball. From our study, the timing accuracy in the Single-speed condition was not necessarily applied to the accuracy when the TTC was variable. However, this aspect might be overlooked in an actual sports practice and players might practice hitting in a situation in which the

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TTC could be anticipated. Thus, it is beneficial to train to discriminate differences of ball speed and to hit the ball with fixed and short movement duration by modulating the moment of swing initiation.

In summary, we found that there is an interpersonal variability in terms of onset and duration control. The onset control group outperformed the duration control group in temporal accuracy. Additional results suggest that the use of onset control strategy is limited by a perceptual and motor function.
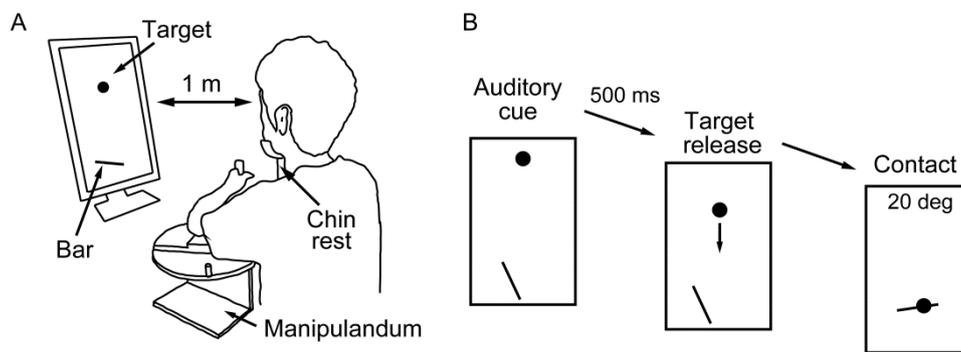
Fig. 3.1 Experimental setup and protocol. (A) Configuration of experimental apparatus. Participants rested their heads on the chin rest and placed their left forearms on the manipulandum. The experimental task was to hit the moving target with the bar controlled by elbow extension. (B) Time sequence of one trial. A warning auditory cue was presented followed by an interval of 500 ms and then the target was released downward. A positive value of constant error (CE) indicates early contact and a negative value indicates late contact.

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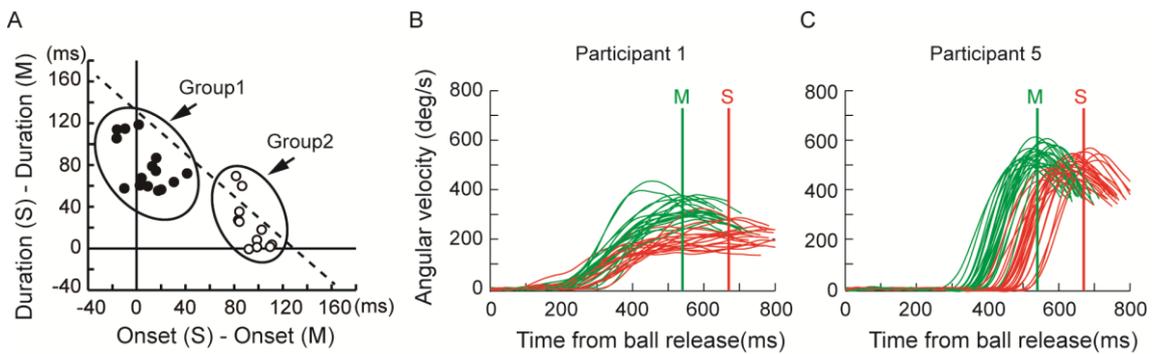
Fig. 3.2 Differences in control strategy between participants in the "slow or medium" condition. (A) Distribution of delta onset and delta duration of all participants. The diagonal dashed line represents optimal compensation for the 130 ms gap in the TTC between faster and slower ball speeds. The distribution of delta onset became bimodal and the participants were divided into two groups: Group 1 (filled circles) mainly modulated their movement duration and Group 2 (open circles) mainly modulated their movement onset. (B), (C) For two participants, typical angular velocity profiles from elbow angle data for slow (red) and medium (green) speeds are plotted. Participant 1 (Group 1) started their movement at approximately the same moment and exhibited the different velocity profiles between target speeds, whereas participant 5 (Group 2) consistently changed the moment of movement onset according to the target speeds.

Table 3.1 Means and Standard Deviation for Basic Kinematic Data in Each Condition such as Movement Onset, Movement Duration, Peak Angular Velocity (Peak_vel) and Angular Velocity at Contact Time (Cont_vel).

	Condition						
	Slow or Medium		Medium or Fast		Single speed		
	Slow	Medium	Medium	Fast	Slow	Medium	Fast
Onset (ms)							
G1	267 ± 50	259 ± 37	225 ± 51	213 ± 33	385 ± 68	288 ± 38	214 ± 24
G2	439 ± 35	345 ± 26	302 ± 42	247 ± 17	469 ± 46	342 ± 34	232 ± 13
Duration (ms)							
G1	382 ± 43	304 ± 34	293 ± 37	237 ± 35	286 ± 58	252 ± 43	218 ± 33
G2	223 ± 40	201 ± 19	230 ± 36	185 ± 13	208 ± 34	204 ± 29	187 ± 12
Peak_vel (deg/s)							
G1	255 ± 28	335 ± 41	329 ± 42	460 ± 65	366 ± 98	405 ± 95	484 ± 85
G2	478 ± 95	526 ± 68	461 ± 85	575 ± 47	518 ± 97	525 ± 95	562 ± 50
Cont_vel (deg/s)							
G1	235 ± 33	318 ± 47	296 ± 51	437 ± 75	347 ± 100	382 ± 98	451 ± 100
G2	459 ± 91	502 ± 71	430 ± 93	543 ± 60	496 ± 94	506 ± 97	538 ± 50

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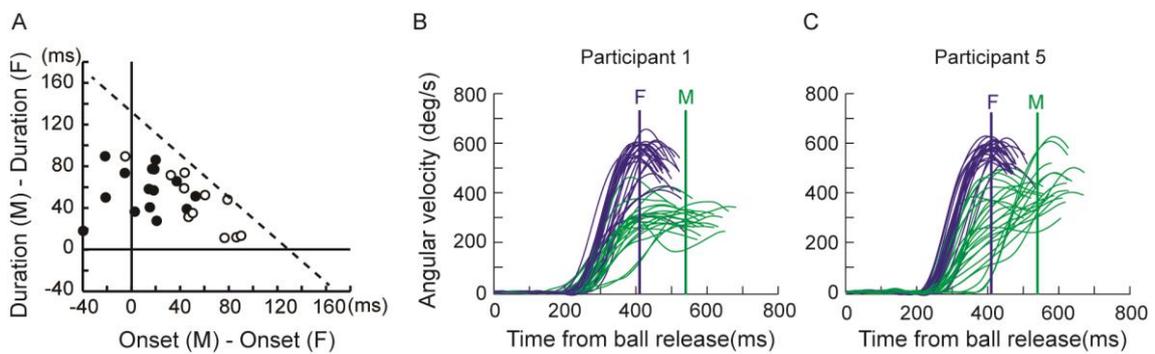
Fig. 3.3 Differences in control strategy between participants in the "medium or fast" condition. (A) Distribution of delta onset and delta duration of all participants. In contrast to the first experiment, the delta onset became a normal distribution. Participants in Group 2 in the first experiment (open circles) reduced the delta onset although participants in Group 1 largely maintained the delta onset. (B), (C) For the same two participants presented in Fig. 2, typical angular velocity profiles for medium (green) and fast (blue) speeds are plotted. Participant 1 exhibited similar profiles of angular velocity compared to the first experiment, whereas participant 5 changed the control strategy and started the movements at approximately the same time in many trials.
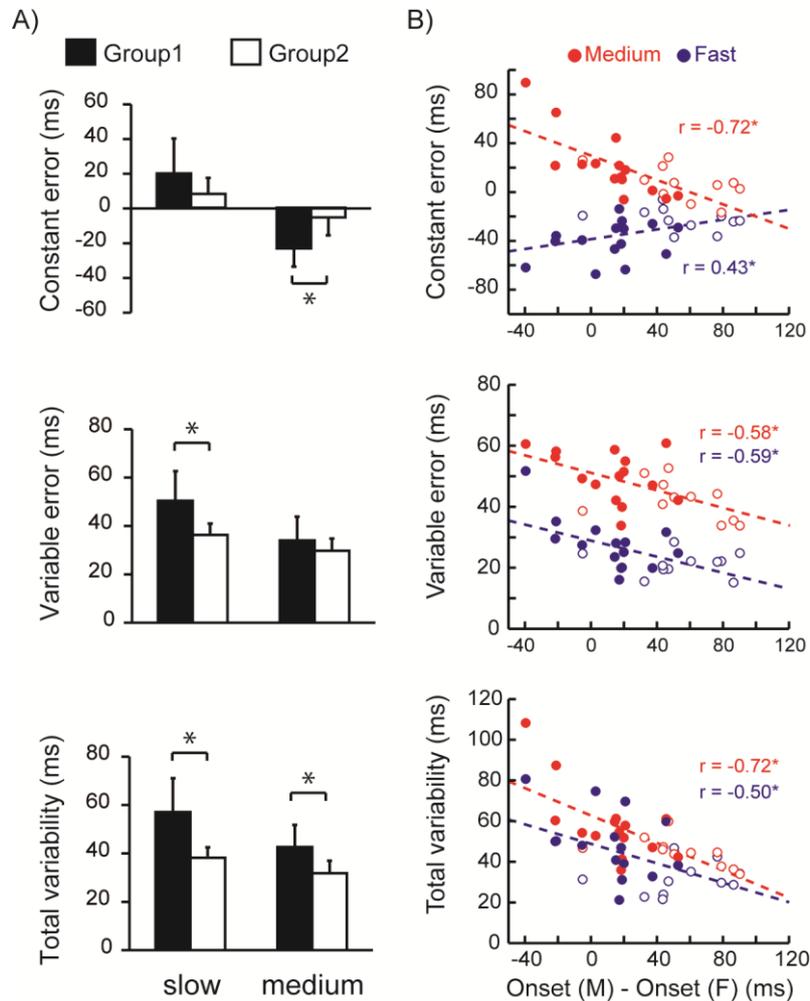
Fig. 3.4 Task performance in the first experiment (A) and the second experiment (B). Each row of the graph shows constant error (top), variable error (middle), and total variability (bottom) of Group 1 (filled bars and circles) and Group 2 (open bars and circles) defined in the first experiment. In the first experiment, control strategies were divided and temporal accuracies were compared between the two groups. In the second experiment, the control strategy did not clearly polarize and correlations between delta onset and temporal accuracies were analyzed. The asterisks indicate a significant difference between groups or correlation (*p < 0.05). The error bars refer to ± 1SD for each group.

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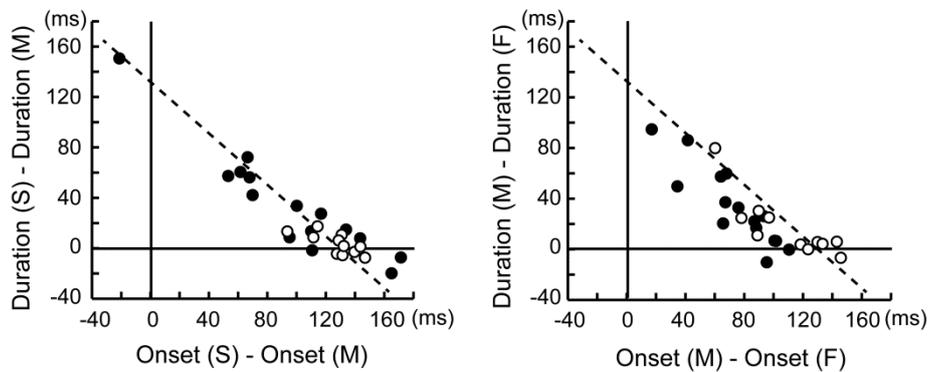
Fig. 3.5 Control strategy in single-speed conditions. The scatter plots represent the distribution of delta onset and duration compared with the slow and medium condition (left panel) and the medium and fast condition (right panel). The diagonal dashed line represents optimal compensation for the 130 ms gap of the TTC between faster- and slower-target speeds. The filled circles represent Group 1 and the open circles represent Group 2 based on the first experiment. Although the distribution of the delta onset became a normal distribution, participants in Group 1 employed a wide range of combinations of movement onset and duration whereas most of the participants in Group 2 kept their movement duration constant between target speeds.

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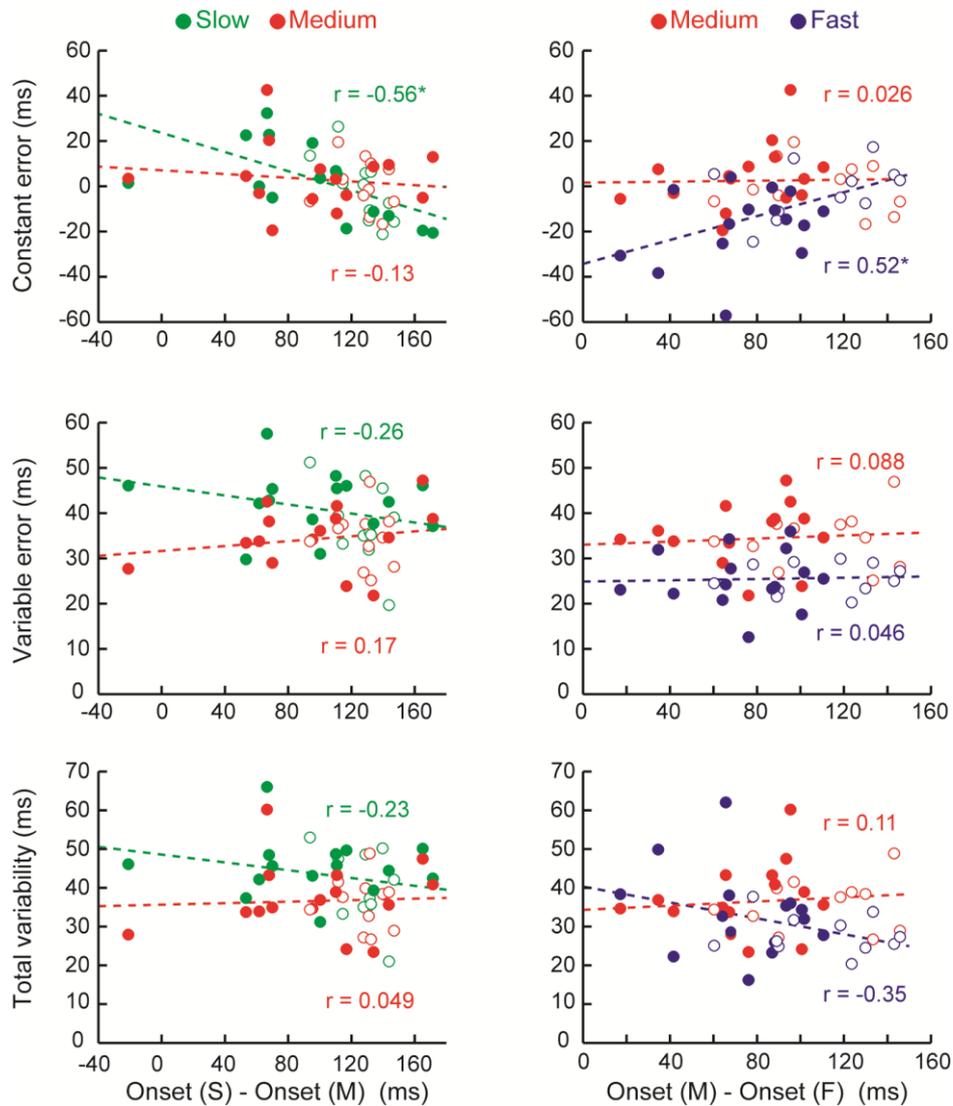
Fig. 3.6 Task performance in single-speed conditions. Each panel shows constant error (top), variable error (middle), and total variability (bottom) for Group 1 (filled circles) and Group 2 (open circles) in single-speed conditions. The asterisks indicate a significant correlation between delta onset and temporal accuracy (*p < 0.05). Note that significant correlations were observed only in the constant error.
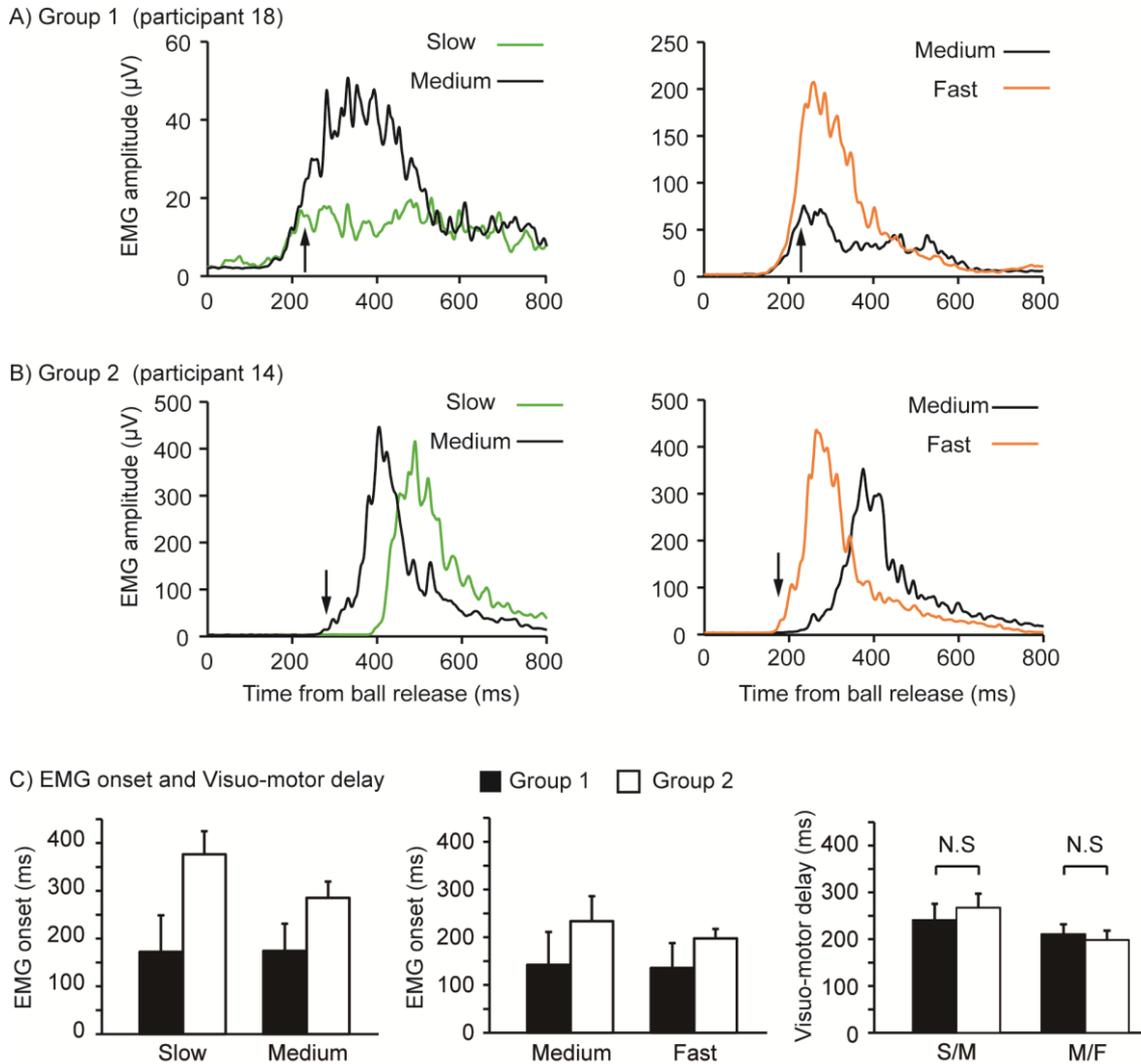
Fig. 3.7 Electromyography (EMG) onset and online correction latency. The ensemble averaged EMG amplitude in the extensor muscle from one participant of Group 1 (A) and Group 2 (B) in the slow or medium condition (left) and the medium or fast conditions (right). The black arrows express the time at which the EMG amplitudes first deviate between the faster- and slower-speed trials indicating the visuomotor delay for the discrimination of target speed. (C) The mean EMG onset and visuomotor delay is indicated by the black arrows. Note that differences between the EMG onsets and the visuomotor delay in Group 1 were around 70 ms. The error bars refer to ± 1 SD.

CHAPTER 4

SUBTHRESHOLD EXCITABILITY MODULATION OF THE SUBCORTICAL MOTOR CIRCUIT CIRCUMVENTS THE TIME CONSTRAINT IN MOVEMENT-INITIATION TIMING

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4.1. Introduction

In our daily lives, we have to control moments of movement onset to successfully interact with our surrounding environment, such as hitting or catching a moving object. In particular, when movement duration is extremely short (rapid interception task), efficacy of online feedback is marginal and the timing of movement onset is crucial for successful interception (see Tresilian, 2005; Zago et al., 2009 for reviews). Under a situation in which the speed of the moving target is fast and variable, we have to discriminate the target speed and modulate the moment of movement initiation according to the target speed. In spite of the severe time constraint in rapid interception tasks, humans are capable of discriminating the target speed and controlling the timing of movement initiation (Ijiri et al. 2014, accepted). Here, we sought to investigate how our central nervous system overcomes severe time constraints to accurately control the moment of movement initiation.

Movement initiation and inhibition is modeled as an interactive race between stop-and-go processes (Logan et al., 1984; Boucher et al., 2007). In this model, an intended movement is initiated when an activation of the go process reaches a threshold, whereas the movement is inhibited when the stop process prevents the go process from reaching the threshold. In a choice reaction-time task, there are multiple response choices and both the preprogramming of a motor command and activation of the go process cannot occur before presentation of an imperative stimulus. In go/no-go task, although preprogramming is possible because the required response is known in advance, the activation of the go process is facilitated after the imperative stimulus.

In a rapid interception task, the motor command can be preprogrammed before movement initiation or even before the target presentation (Gray,

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2002a; Tresilian and Plooy, 2006) similar to go/no-go task. In terms of a traditional framework of the information-processing stage (Schmidt and Lee, 2011), the activation of the go process in a rapid interception task appears to start after stimulus identification (i.e., discrimination of target speed). However, considering the relatively long choice reaction time, the process of speed discrimination is probably time-consuming. Thus, there does not seems to be enough time for serial processing of speed discrimination and activation of the go process according to the target speed.

Alternatively, a parallel processing of pre-activation of the go process and speed discrimination seems to be feasible in light of the interactive race model. In most rapid interception tasks, the time when a target begins to move can be anticipated using some movement-related cues such as opponent's pitching motion in cricket or baseball (i.e., anticipation skill as reviewed in Müller and Abernethy, 2012). Thus the go process might be able to be pre-activated before speed discrimination relative to the faster speed of the target. If the target speed was slower than anticipated, the activation of the go process would be inhibited by the stop process to prevent a movement from being inaccurately initiated. The involvement of inhibitory control has been suggested in the timing of button-press, coincidence-anticipation tasks using electroencephalography (EEG) recordings (Nakamoto and Mori, 2012). In this study, participants have to modulate the moment of button-press to adjust to deceleration in the target speed. The EEG data from the frontal area of the brain indicates that baseball experts have a high ability to detect this deceleration and inhibit an incorrect response.

The aim of the current study was to investigate whether the pre-activation of the go process and inhibitory control contribute to the circumvention of time constraints in movement initiation of rapid interception tasks. To test this, we used a very loud startling acoustic stimulation (SAS), which can

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investigate the activation level of the subcortical motor circuit (see Carlsen et al., 2011, 2012; Valls-Solé, 2012 for reviews) while our participants were performing a rapid interception task with a severe time constraint in which fast and variable target speeds were anticipated.

Recently, an SAS has been used to noninvasively investigate the preparation level of the subcortical motor system. It has been found that the SAS is capable of eliciting not only a reflexive startle response in the sternocleidomastoid (SCM) but also an early release of a preprogrammed motor command within a much shorter latency from the SAS presentation (< 70 ms: StartReact) (Valls-Solé et al., 1999).

Carlsen and colleagues proposed a subcortical triggering model for the mechanism of the StartReact (Alibiglou and MacKinnon, 2012; Carlsen et al., 2012). This model assumes that an SAS increases the neural excitability of pontomedullary reticular formation (PMRF) and gives input through an ascending reticulo-thalamo-cortical pathway, which triggers the cortically stored motor program. According to this model, the incidence and amplitude of the startle reflex and the StartReact would indicate a neural excitability of the subcortical motor circuit (McDowell et al., 2006; Maslovat et al., 2012), including the structures usually involved in movement initiation.

The time course of movement preparation is affected by temporal resolution of the response-timing information. When the temporal resolution is low such as that in a simple reaction-time task, the excitability of the subcortical motor circuit is increased well in advance of the imperative "go" stimulus and an SAS that is presented 1500 ms prior to the imperative stimulus is able to evoke the StartReact. However when the temporal resolution is high, such as that in a coincidence-anticipation task, the increase in the excitability is delayed less than 200 ms prior to the anticipated response time (Carlsen et al., 2008; Carlsen and Mackinnon, 2010) and the excitability is gradually

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increased in anticipation to the response time (Marinovic et al., 2013). Therefore, if the pre-activation of the go process occurs at times with faster target speeds, then this subthreshold activation would be detected by an SAS.

4.2. Methods

(i) Participants

Seventeen healthy male volunteers participated in the experiments (ages: 27.5 ± 4.7 years). All were right-handed and had normal or corrected-to-normal vision. They gave informed consents prior to the participation in the study. Ethical approval for this study was granted by the Ethical Committee of The University of Tokyo (approval number: 274).

(ii) Exclusion criteria

It has been reported that the StartReact is not observed in everyone (Carlsen et al., 2004). Before the main experimental session, we examined the sensitivity of the startle response using a simple reaction-time task. In the results, three participants did not show reliable startle responses in the sternocleidomastoid (SCM) (i.e., EMG onset, which is shorter than 120 ms from an SAS presentation (Carlsen et al., 2011)). In this study, because we were interested in the neural mechanism for the timing control of movement initiation, we excluded the data of participants who could not consistently change their timing of movement initiation according to the target speeds. We monitored the movement onset and duration of each trial to determine whether the participants consistently modulated their movement onset according to the target speeds. Four participants were excluded due to large variability in their movement duration. Therefore, final analyses were

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conducted based on data from ten participants (ages: 26.2 ± 5.1 years).

(iii) Apparatus and task

The participants sat on chairs and placed their chins on a chin rest to stabilize their face positions. A computer monitor (23.6 inches, 1920 × 1080 pixels and 120 Hz refresh frequency) was set at a distance of 1.0 m from participants' faces (Fig. **4.1**A). The participants rested their left forearms in a semi-pronation position on a manipulandum that measured the elbow-angular displacement with a potentiometer. Participants then gripped a metallic rod attached to the manipulandum with their shoulder flexed approximately 75 degrees and abducted 20 degrees. The rotation of potentiometer was converted to the same degrees of bar (bat) rotation. A black virtual target (ball) with a diameter of 10.9 mm (0.62°) was projected on the monitor. The distance between the point of target release and the axis of the bat rotation was 27.2 cm.

The sequence of a trial is presented in Fig. **4.1**B. The experimental task was to hit the moving target with the virtual bar. When participants set the bar to an initial position and stayed for one second, an auditory cue (60 dB, 1000Hz, 100 ms) was provided. The initial position was indicated by a mechanical stop located -65 degrees from the desired hit point. The target was then released downward after a foreperiod of 500 ms. A horizontal line with the axis of rotation was defined as the desired hit point and participants were instructed to intercept the target as close as possible to the desired hit point. There were two moving target speeds: Fast (TTC was 500 ms) and Slow (TTC was 800 ms).

(iv) Startling acoustic stimulation (SAS)

The startling acoustic stimulus (SAS) was generated by a customized program written in LabVIEW software (National Instrument), which produced

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broadband white noise (duration; 50 ms, rise time; 1 ms). The signal was amplified and presented with an intensity of 123 ± 1 dB through a loudspeaker (DSR112, YAMAHA) placed 50 cm behind the head of the participants. The sound intensities were measured using a sound-level meter placed 5 cm laterally from participants' heads. The stimulus was presented 150 ms after the initiation of target displacement.

(v) Experimental design and procedure

The main experimental session consisted of two conditions: The sequence of the experimental sessions is presented in Fig. 4.1C.

1) Paired-speed (PS) condition in which Fast- and Slow-speed targets were presented pseudo-randomly and participants had to compensate the TTC difference of 300 ms by mainly changing the onset of movement. Participants performed 80 trials in total and the SAS was presented in 8 trials (10%), with the restriction that no two startle trials were presented within every five trials.

2) Single-speed (SS Slow) condition in which only a slow-speed target was presented. Participants performed 20 trials without an SAS presentation as a practice session to wash out the motor set in the PS condition and 80 trials as experimental sessions. The SAS was presented in 8 trials (10%). In both conditions, the SAS was presented as one out of ten trials in slow-speed trials to evaluate the effect of a potentially anticipated fast-speed target on the excitability of the subcortical motor circuit during premotor time. The two conditions were presented in the order described above to determine the participants' timing strategy according to the time constraints of the PS condition.

Prior to the main experimental session of the PS condition, participants performed a practice session without the SAS presentation. To become

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familiar with the task and stabilize their control strategy, all participants performed at least 60 trials and 110 trials at most. After every trial, movement duration and spatial-constant error were provided for the participants. The error was defined as the bat angle at which the target and bar made contact. We monitored the movement onset and duration of each trial to determine whether the participants employed the strategy to mainly change movement onset or duration. In the PS condition, participants were instructed to maintain the same timing strategy as in the practice session (i.e., to maintain the same movement duration as in the practice session).

In many previous studies involving the use of an SAS, repeated exposure resulted in a startle-response habituation (Valls-Solé et al., 1997; Schicatano and Blumenthal, 1998). The habituation occurs even when participants prepare a movement in a reaction-time task, although the readiness for a movement decreases the habituation (Valls-Solé et al., 1997; Carlsen et al., 2003). To assess the effect of SAS habituation on the experimental results, we conducted an additional 40 trials of the PS condition (PS_{post}) after the SS_Slow conditions. The probability of the StartReact effect was compared between the PS_{pre} and PS_{post} condition and the SS_Slow and PS_{post} condition.

Finally, the Single-speed (SS_Fast) condition in which only the fast-speed target was presented was conducted in six out of ten participants. This condition was conducted to investigate whether inhibition of the subcortical motor circuit in the PS condition occurs at the SAS presentation time compared with the probability of the StartReact effect between PS and SS_Fast conditions.

(vi) **Recording system**

Electromyography (EMG) signals were acquired using a double differential

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surface electrode (DE-3.1, Delsys) with an analogue bandpass filter (20–450 Hz) from the bellies of triceps brachii (TB), and sternocleidomastoid (SCM). The other setup was the same as that of study 1 (see Recording System in Chapter 3).

(vii) Data reduction

EMG onset was defined as the point at which full-wave rectified EMG activities increased to more than 3 SDs above baseline (mean of 100 ms of EMG activity before target displacement). EMG and movement onset were detected using a computer algorithm and then verified manually by superimposing a line indicating the threshold on the EMG data (a method recommended in Carlsen et al. (2011)). Movement onset was defined as the time between initiation of target displacement and the first moment at which the elbow angle changed more than 0.2° from the initial position. Movement duration was defined as the time between movement onset and the moment at which the elbow angle reached the desired hit point.

(viii) Statistics

The probability and latency of startle response were analyzed using a two-way 2 (muscle) × 3 (condition) repeated measures of ANOVA to test the effect of the experimental condition and the difference between the StartReact and the startle reflex. Post-hoc comparisons were performed with Tukey HSD tests ($p < 0.05$). For analyses of the habituation effect, the incidence of the StartReact in the triceps brachii (TB) was compared between PS_{pre} and PS_{post} and between SS_Slow and PS_{post} using a paired t-test ($p < 0.05$).

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4.3. Results

(i) Basic kinematic data

The results of movement onset and movement duration in the control trials
are shown in Table 4.1. Considering that the SAS was presented 150 ms after
the target release, the moment of the SAS presentation was about 400 ms
prior to movement onset in the slow trials of PS and SS conditions. Carlsen
and colleagues reported that the StartReact is not consistently evoked by an
SAS until there is less than 200 ms prior to the intended response time
(Carlsen et al., 2008; Carlsen and Mackinnon, 2010). Therefore, if the SAS
evoked the StartReact in these conditions, the involvement of pre-activation
of the motor circuit would be indicated.

(ii) Typical results and averaged EMG

Fig. 4.2 shows representative startle trials in each condition. In a slow trial of
the PS condition (top panel), the SAS evoked both the StartReact and startle
reflex with a latency of about 50–80 ms from the SAS presentation. The
movement onset was also markedly shortened compared with the control trial.
On the other hand, in the SS_Slow condition (middle panel), the SAS evoked
only startle reflex in SCM and did not elicit prepared motor command. The
participant started their movement relatively at the same moment to the
control trial. Similar to the result in slow trial of PS condition, both
StartReact and startle reflex were evoked in SS_Fast condition (bottom
panel).

Fig. 4.3 shows representative averaged EMG amplitudes of TB across each
condition from a single participant. The results displayed in Fig. 4.2 were
consistently observed throughout the experiment and almost the same
component to SS_Fast trials was elicited by the SAS in the PS_Slow trials.

These results indicate that in slow trials of the PS condition, the participant prepared a motor command in advance and the subcortical motor circuit was pre-activated in the timing of the fast-speed target.

(iii) Probability of the StartReact and startle reflex

Similar results were consistently obtained in all participants. Average probabilities of the StartReact in the TB and the startle reflex in the SCM are shown in Fig. 4.4. Two-way 2 (muscle) × 3 (condition) repeated measures of ANOVA found a significant main effect for muscle [$F(1,9) = 8.91$, $p < 0.01$] and for condition [$F(2,18) = 27.4$, $p < 0.001$]. There was also a significant interaction between the variables [$F(2,18) = 9.58$, $p < 0.001$]. A post-hoc analysis of this interaction revealed that the probability of a TB response of the SS_Slow condition (15.0 ± 18.4 %) was lower than that of the PS_Slow condition (80.2 ± 13.2 %, $p < 0.001$) and the SS_Fast condition (93.8 ± 10.5 %, $p < 0.001$). On the other hand, the probability of the startle reflex in the SCM was not significantly different between each condition (PS_Slow: 89.2 ± 14.7 %, SS_Slow: 68.8 ± 34.0 %, SS_Fast: 85.4 ± 25.5 %, $p > 0.282$).

(iv) Response latency in startle and control trials

The average EMG onset in control trials was as follows: PS_Slow; 473±39 ms, PS_Fast; 280±10 ms, SS_Slow; 499±30 ms, SS_Fast; 243±30 ms. EMG activity onset in the TB and the SCM in startle trials are shown in Fig. 4.5. It should be noted that for the latency calculation, the trials in which the SAS did not evoke the startle reflex or the StartReact were not included. Two-way 2 (muscle) × 3 (condition) repeated measures of ANOVA found a significant main effect for muscle [$F(1,9) = 43.1$, $p < 0.001$] and for condition [$F(2,18) = 14.4$, $p < 0.001$]. There was also a significant interaction between the variables [$F(2,18) = 6.27$, $p = 0.004$]. A post-hoc analysis revealed that in the

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PS_Slow and SS_Slow conditions, the EMG onset of the SCM (PS_Slow: $214\pm$ 12 ms, SS_Slow: 218 ± 12 ms) was faster than that of in TB (PS_Slow: 238 ± 10 ms, SS_Slow: 260 ± 18 ms). Moreover, the EMG onset of the TB was significantly different between each condition (PS_Slow: 238 ± 10 ms vs SS_Slow: 261 ± 18 ms, $p = 0.021$). On the other hand, the EMG onset of the SCM was not significantly different between each condition ($p > 0.716$).

*(v) **Effect of habituation on the StartReact and startle reflex***

There may be a possible explanation that habituation for the SAS produced the difference in startle-response probability across conditions because the sequence of conditions was not counterbalanced. To rule out the potential confounding factor, we compared the probability of StartReact in the TB between PS_{pre} and PS_{post} sessions and SS_Slow and PS_{post} sessions (Fig. 4.6). As a result, the probability in PS_{pre} (91.1 ± 13.3 %) was significantly higher than that in PS_{post} (55.6 ± 27.3 %, $t = 3.74$, $p = 0.006$) and the probability in PS_{post} was significantly higher than SS_Slow (15.0 ± 18.4 %, t = 5.09, p < 0.001). This result revealed that although there was a significant habituation effect to the SAS, it did not reject the main effect of the experimental condition. Additionally, the incidence of the StartReact in PS_{post} condition was significantly lower than that in the SS_Fast condition (93.8 ± 10.5 %, $t = 2.71$, $p = 0.042$). Because the habituation effect would be larger in the SS_Fast than in the PS_{post} due to the order of the experimental session, this result suggests the involvement of inhibition of the go process in the PS_{post} condition at the timing of the SAS presentation.

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4.4. Discussion

In the experiments reported here we sought to test whether pre-activation of the go process and inhibitory control contributes to the circumvention of time constraints in movement initiation of a rapid interception task. To test this hypothesis, we used a StartReact paradigm and assessed the excitability of the subcortical motor circuit while our participants were performing a rapid interception task in which they had to adjust the timing of movement onset according to target speeds.

(i) Anticipatory pre-activation of the subcortical motor circuit

It has been found that in an anticipation-timing task, the go process is activated just 200 ms prior to movement onset (Carlsen et al., 2008; Carlsen and Mackinnon, 2010). In these studies, when an SAS was presented 500 ms prior to movement onset, the probability of the StartReact was less than 20%. In contrast, when the SAS presentation was 150 ms prior to movement onset, the probability of the StartReact was more than 90%. These results were quite consistent with our results in single-speed conditions. In the SS_Fast condition, where the SAS was presented about 150–200 ms prior to movement onset, the StartReact was evoked with a high probability (93.8 ± 10.5 %), which suggested that the subcortical excitability was enhanced for the fast target. On the contrary, a low probability of StartReact in the SS_Slow condition (15.0 ± 18.4 %), where the SAS was presented 400 ms prior to movement onset, suggests that the subcortical motor circuit was not yet activated at that timing.

   In both PS_Slow and SS_Slow conditions, the moment of SAS presentation was about 400 ms prior to movement onset, whereas in the PS_Fast and SS_Fast conditions, it was about 150–200 ms prior to movement onset. However, in slow trials in the PS condition, an SAS consistently elicited the StartReact (80.2 ± 13.2 %). The

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only difference between the slow trials in the SS_Slow and PS conditions was the existence of potentially anticipated fast-speed trials. Thus, the high incidence of the StartReact in the PS_Slow condition provides evidence of anticipatory pre-activation of the go process for the timing of the fast-speed target. In addition, EMG onset of the fast-speed trial in the PS condition was 243 ± 30 ms, which is shorter than human spatial choice-reaction time (Anzola et al., 1977; Delignières, D., Brisswalter, J., & Legros, 1994; Mori et al., 2002). Thus, the anticipatory pre-activation would have contributed to the circumvention of the severe time constraint in movement-onset decision making.

(ii) *Involvement of inhibitory control in delaying the movement onset*

This anticipation benefit could be a risk of incorrect movement initiation for the timing of a potentially anticipated fast-speed target. However, our participants successfully adjusted their timing of movement onset according to target speeds. The incidence of the StartReact in the PS_{post} condition (55.6 $\pm$ 27.3 %) was significantly lower than that of the SS_Fast condition (93.8 $\pm$ 10.5 %) although in both conditions, the fast-speed target was anticipated. Moreover, considering the order of the experimental session, habituation to the SAS would be larger in the SS_Fast condition. Therefore the low incidence of the StartReact in the PS_{post} condition suggests an involvement of inhibitory control of the subcortical motor circuit at the timing of the SAS presentation in the PS condition (i.e., about 200 ms before movement onset of the fast-speed trial in the PS condition). Fig. **4.7** shows a schematic of this explanation for the (A) SS_Fast condition, (B) the slow trial in the PS condition, and (C) the SS_Slow condition. To our knowledge, our results have shown for the first time that modulation of the activity in the subcortical motor circuit are involved in delaying intended movement onset.

(iii) Different pathways mediating the StartReact and the startle reflex

In the current study, the incidence and latency of the StartReact in the triceps brachii (TB) was affected by the experimental conditions (Fig. 4.4). In contrast, those of the startle reflex in the sternocleidomastoid (SCM) were not significantly changed across conditions. Moreover, the latency of EMG onset evoked by the SAS was different between the TB and the SCM (Fig. 4.5). These differences strongly indicate the involvement of different pathways mediating the StartReact and startle reflex.

It is established that the acoustic startle reflex is mediated by a cluster of giant neurons in the ventrocaudal part of the nucleus reticularis pontis caudalis (RPC) of the pontine reticular formation (Yeomans and Frankland, 1995; Koch, 1999). The RPC neurons are excited by an SAS via the cochlear nucleus and then produce, along the reticulo-spinal tract, a reflexive EMG response in the SCM. On the other hand, many previous studies have suggested that the StartReact is triggered through an ascending reticulo-thalamocortical pathway including the primary motor cortex (Skinner et al., 2004; McDowell et al., 2006; Alibiglou and MacKinnon, 2012; Carlsen et al., 2013; Marinovic et al., 2014). Therefore we presume that excitability modulation of the subcortical motor circuit would mainly arise from the thalamo-cortical pathway. However, because the motor networks in the brainstem also receives efferents from the basal ganglia, and particularly from the substantia nigra par reticulate (SNr) (Moriizumi et al., 1988; Inglis and Winn, 1995; Hikosaka et al., 2000; Takakusaki et al., 2003), it is possible that the excitability of RPC neurons were also affected by the context-dependent motor preparation. Actually, in many startle trials in the current study, EMG amplitude in the SCM was smaller in the SS_Slow condition than that in the SS_Fast and PS_Slow conditions (see a typical example in Fig. 4.2). Moreover, some previous studies also have reported the

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context-dependent modulation of the startle reflex in SCM (Kumru et al., 2006; Maslovat et al., 2012). Therefore other cortico-cortical networks are likely to be involved in the context-dependent modulation of the StartReact. In the next section, we discuss the possible neural mechanisms of the modulation of the StartReact.

(iv) *Interactive race between the go and stop process*

Movement initiation and inhibition is modeled as an interactive race between go and stop processes (Logan et al., 1984; Boucher et al., 2007). In this model, an intended movement is initiated when an activation of the go process reaches a threshold, whereas the stop process suppresses the movement initiation by strongly inhibiting the activation of the go process and preventing the go process from reaching the threshold. We presume this race model could be extended to explain the excitability modulation in the subcortical motor circuit.

Recently, Schmidt et al. (2013) have found that two distinct pathways in the basal ganglia represent the race between these two processes. Specifically, striatal direct-pathway neurons promote movement (go process) by inhibiting the substantia nigra par reticulate (SNr) (Hikosaka et al., 2000; Kravitz et al., 2010). On the other hand, the subthalamic nucleus (STN) neurons work as a stop process by exciting the SNr neurons (Alexander et al., 1990; Nambu et al., 2000, 2002). The STN neurons seem to receive input from the inferior frontal cortex (IFC) and pre-supplementary motor area (pre-SMA) (i.e., hyperdirect pathway) for suppression of intended movement (Aron et al., 2003; Aron and Poldrack, 2006; Chambers et al., 2006; Duann et al., 2009). The relative timing of the two inputs to SNr determines a successful cancellation of intended actions (Schmidt et al., 2013). In addition, there is another excitatory pathway to inhibit movement from striatum to STN (i.e., indirect

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pathway). Sano et al., (2013) reported that this pathway contributes to inhibiting an already initiated movement. Therefore we speculate that this pathway is not involved in the onset control in the current study. Projection from SNr to thalamus has a GABAergic inhibitory projection (Kilpatrick et al., 1980; Hikosaka and Wurtz, 1983) and the two distinct pathways in the basal ganglia might modulate the activity in the thalamo-cortical motor pathway. In addition, there is some evidence that the thalamus is responsible for the movement initiation providing ascending input to the motor-related cortical area (Haider et al., 1969; Parent and Hazrati, 1995; Kunimatsu and Tanaka, 2010).

As an another possible mechanism, cortico-cortical interaction between the dorsal premotor cortex (PMd) and the primary motor cortex (M1) has been reported (Kaufman et al., 2014). This study has suggested that neural activities in the PMd cancel out a preparatory activity in M1, which enables a state of motor preparation without triggering the motor output. It is possible that this connection inhibits the preparatory activity in the thalamo-cortical pathway and the SAS affected this interaction and disabled the cancellation. Moreover, it has been reported that the prefrontal cortex also contributes to the prepared response inhibition (Konishi et al., 1998; Menon et al., 2001; Kadota et al., 2010), although interaction with other cortical and subcortical areas is unknown and therefore further investigation is needed about the relationship between activities in these areas. Taken together, we presume that the differences in the latency and incidence of the StartReact across experimental conditions in the current study were a result from the modulation in excitability of the thalamo-cortical pathway mediated by the race between the go and stop processes in the basal ganglia. A scheme of the neural mechanism is shown in Fig. 4.8.

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(v) Preprogramming control with continuous online feedback

Finally, there is a long standing debate about preprogramming control and continuous control of rapid interceptive actions (Tyldesley and Whiting, 1975; Bootsma and Van Wieringen, 1990; Tresilian, 2005; Zago et al., 2009). The preprogramming control model proposes that a motor command is entirely preprogrammed prior to the initiation of interceptive action. On the other hand, continuous control model proposes that interceptive movement is continuously updated using sensory information. It now appears that these two controls are not alternatives; the nervous system uses both in a flexible manner (Zago et al., 2009; Brenner and Smeets, 2011). In the current study, the SAS presented 150 ms after the target release triggered a whole interceptive movement. This result indicates the use of preprogramming control and is consistent with previous research (Tresilian and Plooy, 2006), which proved a preprogrammed motor command. Importantly, we also found that when multiple target speeds are anticipated, the timing control of movement initiation was achieved by the subthreshold excitability modulation of the motor circuit. That is, the timing control of initiation of prepared movement is achieved in an ongoing fashion using online visual information.

In conclusion, the data presented in the current study provide evidence that pre-activation of the subcortical motor circuit under a threshold level circumvents a severe time constraint in the timing control of movement initiation in rapid interceptive actions.

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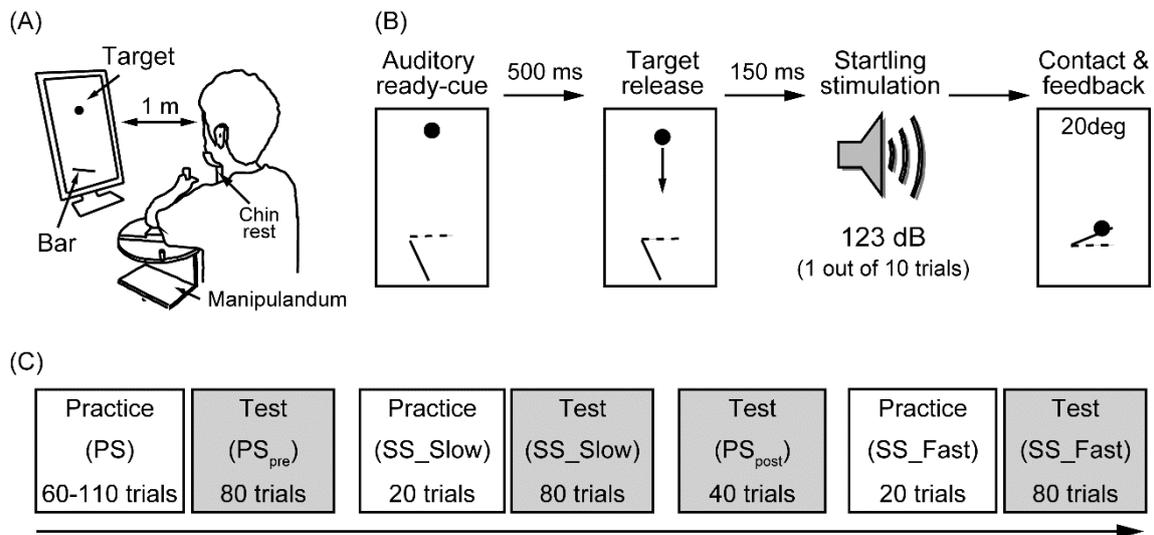
Fig. 4.1. Experimental setup and procedure. (A) Configuration of experimental apparatus. Participants rested their heads on the chin rest and placed their left forearms on the manipulandum. A loudspeaker was placed 50 cm behind the participants' heads to present a startling acoustic stimulation (SAS). (B) Schematic of the trial sequence and stimuli. A warning auditory cue was presented followed by an interval of 500 ms and the target was then released downward. A startling stimulation was presented 150 ms after the target release in one out of ten trials. Visual feedback was provided at the end of every trial. A positive value of constant error (CE) indicates early contact and a negative value indicates late contact. (C) The sequence of the experimental sessions.

Table 4.1 Mean Value of Movement Onset and Duration (mean ± SD ms.)

	PS_Fast	PS_Slow	SS_Fast	SS_Slow
Onset	350 ± 19	553 ± 41	307 ± 24	575 ± 32
Duration	194 ± 23	238 ± 39	212 ± 28	231 ± 36

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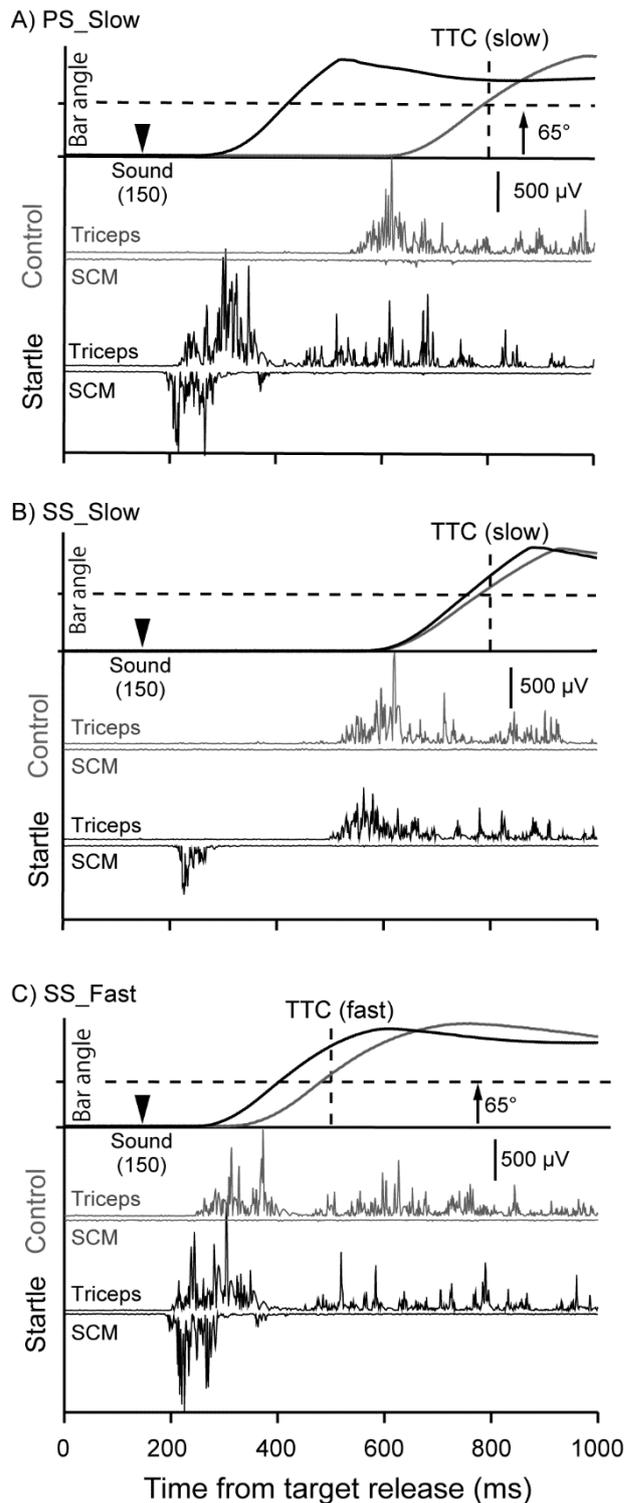
Fig. 4.2. Representative startle trials from one participant. Each panel shows startle trials in PS_Slow (top), SS_Slow (middle) and SS_Fast (bottom) conditions. (A) In the slow trial in the PS condition, the startling acoustic stimulation (SAS) presented 150 ms after the target release evoked both the StartReact in the triceps brachii (TB) and the startle reflex in the sternocleidomastoid (SCM) with the latency about 70 ms (TB) and 50 ms (SCM) from the SAS presentation. Movement onset was also markedly shortened compared with that of the control trial. (B) In the SS_Slow condition, the SAS evoked only a startle reflex in the SCM and did not elicit any voluntary movement. The elbow movement in the startle trial was initiated at almost same time as that of the control trial. (C) In the SS_Fast condition, the SAS evoked both the StartReact and startle reflex and the movement onset was also shortened compared with the control trial.

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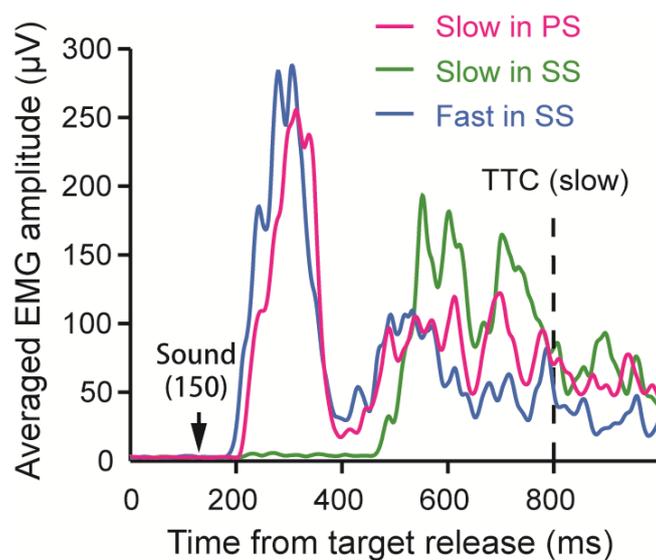
Fig. 4.3. Representative averaged EMG amplitude of triceps brachii (TB) in startle trials from one participant. The startling stimulation consistently evoked the prepared motor command in the slow trial of the paired-speed (PS) condition and the fast trial in the single-speed (SS) condition.
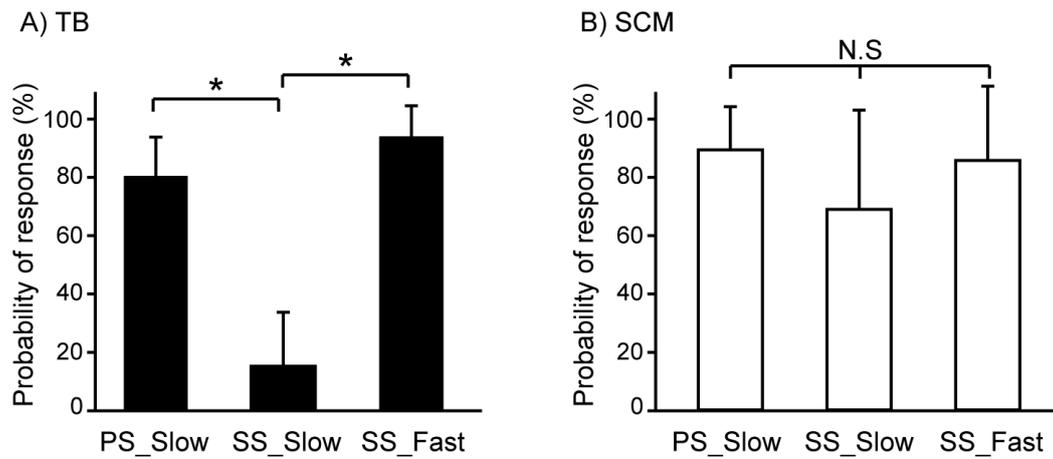
Fig. 4.4. The mean probability value of early activity evoked by the startling stimulation. Activity of the sternocleidomastoid (SCM) was triggered in all conditions, but that of the triceps brachii (TB) was consistently triggered only in the slow or fast condition. The asterisks indicate a significant difference between groups or correlation (*p < 0.01).

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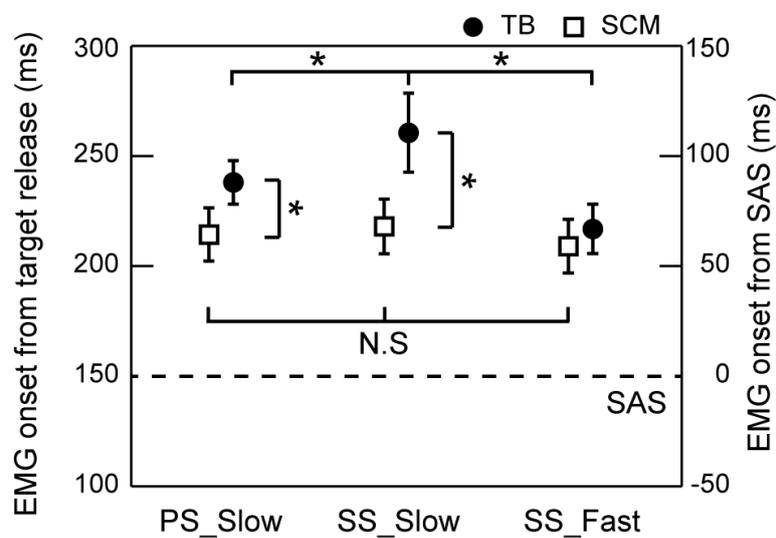
Fig. 4.5. EMG onset in triceps brachii (TB) and sternocleidomastoid (SCM) in startle trials. There was no significant difference in the SCM latency across all conditions. By contrast, the TB latency was significantly different across all conditions. A difference was found between TB and SCM in PS_Slow and SS_Slow conditions. These results indicate a different pathway mediating the StartReact in the TB and the startle reflex in the SCM. It should be noted that these latencies in the TB were markedly shortened compared with the EMG onset in control trials (PS_Slow; 473 ± 39 ms, SS_Slow; 499 ± 30 ms, SS_Fast; 243 ± 30 ms). The asterisks indicate a significant difference between groups or correlation (*$p < 0.05$).

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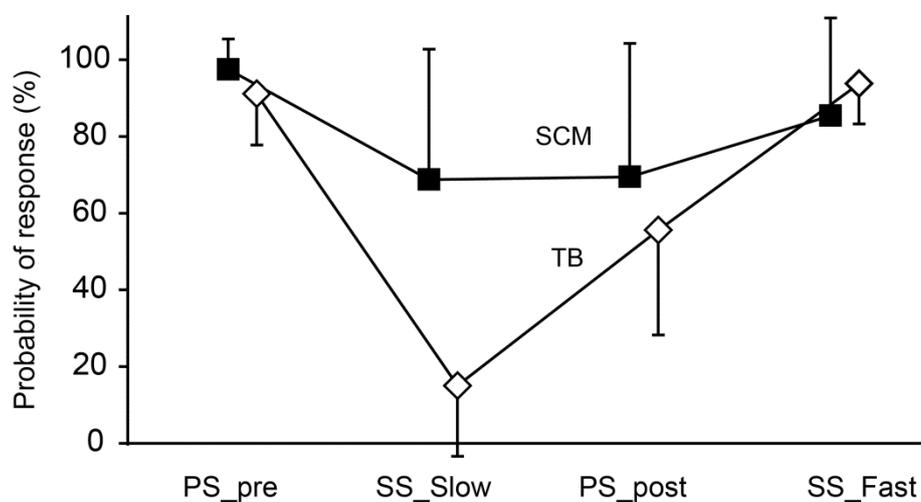
Fig. 4.6. Probability of the StartReact and startle reflex are presented in the order of experimental sessions. The incidence of the StartReact in triceps brachii (TB) significantly decreased in the PS_{post} condition compared to the PS_{pre} condition, which suggests the effect of habituation to SAS. However, the incidence of the StartReact in the SS_Slow condition was significantly lower than in the PS_{post} condition, which indicates that the main effect of the experimental condition on the StartReact probability. In addition, the StartReact probability was significantly higher in the SS_Fast condition than in the PS_{post} condition, which indicates that activation of the go process was inhibited at the timing of the SAS presentation.
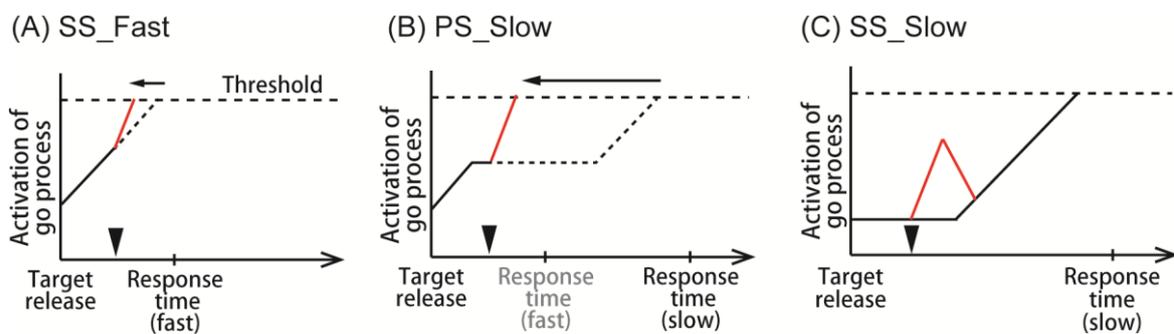
Fig. 4.7. Schematic of subthreshold modulation of the go process activation in (A) SS_Fast condition, (B) a slow trial in the PS condition and, (C) the SS_Slow condition. Dashed lines represent the activation threshold to trigger a prepared motor command. Red lines indicate increased activation by startling acoustic stimulation (SAS). In the SS_Fast and PS_Slow conditions, the activation level is enhanced for the timing of the fast-speed target. In the SS_Slow condition, the activation level is not pre-activated because the fast-speed target is not anticipated.

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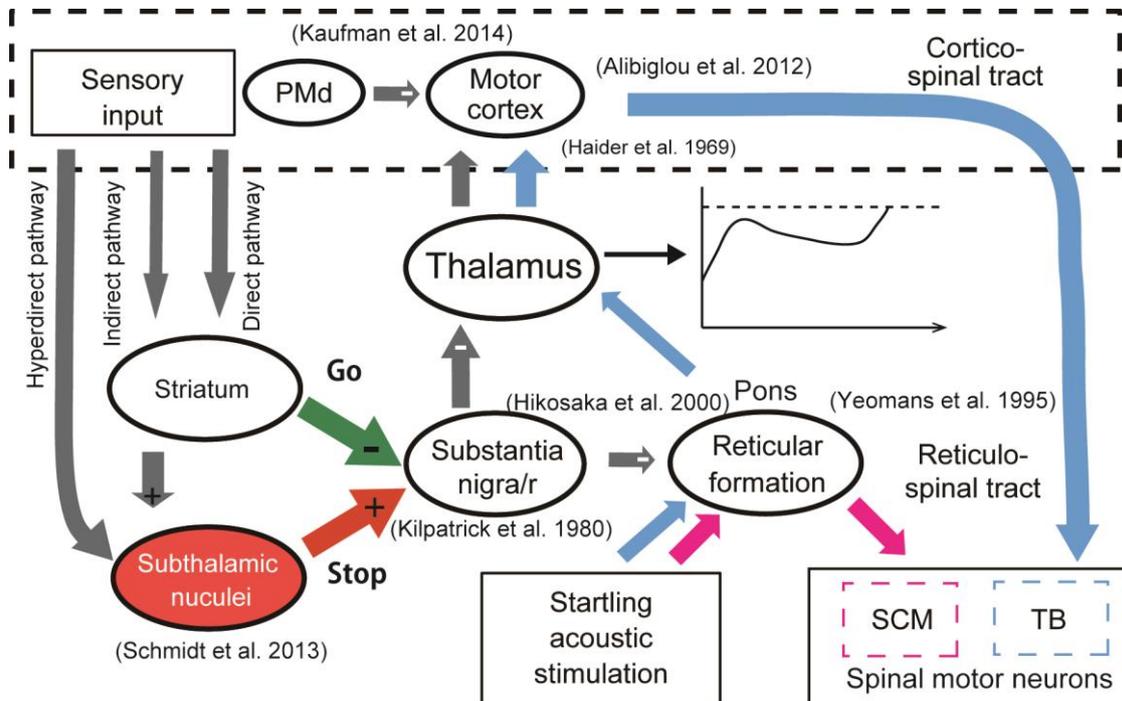
Fig. 4.8 A possible neural mechanism of modulation of excitability in the
subcortical motor circuit. An SAS activates neurons in the pontine reticular
formation and these neurons send descending input to the SCM via the
reticulo-spinal tract. At the same time, ascending input is issued to the thalamic
nucleus. The activation of the thalamo-cortical pathway, which would trigger a
cortically stored motor command, is modulated by the two distinct go and stop
processes in the basal ganglia.

CHAPTER 5

GENERAL DISCUSSION

5.1. Brief summary of the experimental results

In this thesis, two studies were conducted to provide further insight into human visuomotor coordination in a rapid interceptive action. The following findings and suggestions were obtained from these experiments.

(i) Study 1 (Chapter 3)

In the first experiment ("Paired-speed Slow or Medium" condition), we found interpersonal variability in timing-control strategies. Eleven out of 26 participants mainly modulated their movement onset and exhibited a ballistic and bell-shaped angular-velocity profile of an elbow extension movement. On the other hand, 15 participants mainly modulated their movement duration with non-bell-shaped velocity profiles for slower speed target, which suggested the use of online correction.

In the second experiment, which was under a more severe time constraint ("Medium or Fast" conditions), the many of the participants could not maintain the onset-control strategy and their strategies shifted to duration-control strategies. In both the first and second experiments, onset-control strategy outperformed duration-control strategy.

In the third experiment (the Single-speed condition), the same speed target was presented in each block and participants did not need to discriminate the target speed. In this condition, only a small difference in temporal accuracy was observed between participants who used different

control strategies in Paired-speed conditions. This result indicated that cognitive processes relating to speed discrimination of a target and/or decision making of movement onset were the critical factors for temporal accuracy.

(ii) Study 2 (Chapter 4)

In experiment 2, we found that onset control was achieved by a subthreshold excitability modulation of the subcortical motor circuit. This motor circuit might be modulated by a race between two distinct inputs from the striatum (go process) and the subthalamic nucleus (stop process)(Schmidt et al., 2013). From a framework of the interactive race model in which the go process and stop process inhibit each other, disruption of the onset control in the "Medium or Fast" condition seemed to be produced by an insufficient time for the stop process to inhibit the pre-activated go process. We assumed that those who did not use the onset-control strategy took more time to inhibit the motor circuit and they could not hold the prepared interceptive movement. Thus, they started at approximately the same time between faster and slower targets, which resulted in the observed reliance on duration control. Another possible explanation might be that the time available for activation of the stop process was sufficient, however, estimation of the activation timing of the go and stop processes were much less accurate than that of the onset control group. The fact that participants in the duration-control group employed this strategy in the Slow or Medium condition supports this suggestion because there might be relatively enough time in the easily constrained condition.

In the following sections, we make some arguments based on the results from the standpoints of (1) differences between an experimental and an actual sports environment, and (2) practical implications for real-world hitting tasks.

5.2. Differences between experimental and an actual sports environment

(i) Control of temporal and spatial components

In this thesis, we focused only on the temporal aspect of rapid interceptive action. As a result, we found that the process of speed discrimination and the timing control of movement initiation according to target speed are critical factors for temporal accuracy. However, in an actual sports environment such as baseball hitting, a spatial component such as the height of the swing might also be important for task performance. Actually, Gray (2002a) reported that varying ball speeds from pitch to pitch (i.e., a Paired-speed condition in this thesis) resulted in large errors in the height of the swing. Therefore, our experimental results do not deny the efficacy of online correction of the swing in rapid interception. We speculate that temporal error is mainly compensated by the timing of movement onset and spatial error is mainly compensated by online correction. Many non-conscious automatic corrections such as manual response following response (MFR) (Saijo et al., 2005; Amano et al., 2009), automatic pilot (Kadota and Gomi, 2010; Abekawa et al., 2014), and action -blindsight (Christensen et al., 2008) are spatially corrected movements, which would support our speculation. Further investigation is needed about the functional contribution of these non-conscious online corrections for spatiotemporal accuracy in rapid interception.

(ii) Source of visual information for the TTC estimation

In our experimental task, a visual target was projected on a two-dimensional PC monitor, although in many actual interceptive actions a visual target goes through three-dimensional external space. Therefore a different visual source of information would have been used for the TTC estimation in our task

compared with an actual hitting task. Although there is a longstanding debate about the visual source of information for the TTC estimation (reviewed in Zago et al., 2009), no consensus has been reached on this issue. It has been proposed that various kinds of visual information such as the rate of image expansion (Regan and Hamstra, 1993) or optic variable tau (Lee et al., 2001) could not been used effectively in rapid interceptive actions because accurate calculation of these variables is difficult using an initial trajectory of a pitched ball in rapid interception (Zago et al., 2009). On behalf of these variables, batters use prior knowledge about speed and/or trajectory of a pitched ball (Gray, 2002a) and this factor could have been used in our experimental task. Thus, we presume that our results could be generalized in a real-world interceptive task.

(iii) *Single-joint and full-body movement*

In our experimental task, we employed a simplified elbow-extension task, because a multi-joint dynamical task is hard to control in a laboratory environment. However, actual hitting is a sequence of coordinated muscle activity beginning with the lower extremities, followed by the trunk, and terminating with the upper extremities (Shaffer et al., 1993). To what extent is the experimental result from a single-joint movement task applicable to the actual complex motor task?

Gray (2002a) reported that the swing duration of expert baseball players was about 150 ms, which is a similar value of the movement duration in our task. This value was the time from the onset of the bat downward motion to the moment of hitting a baseball. Given that the hip and trunk movement starts much earlier than the initiation of the bat movement, the time from initial hip movement to the moment of hitting was about 300 ms (Shaffer et al., 1993). Therefore, it is strongly indicated that batters would initiate their hip

and trunk movement in every trial whether or not the subsequent arm movement is initiated. If they then decide to hit the baseball, they would not inhibit the kinematic chain and arm movement would be initiated. On the contrary, if they decide to stop or delay the swing initiation, muscle activity in each phase of the kinematic chain would be inhibited. Thus, the onset control using flexible inhibitory control (i.e., the main finding of Chapter 4 in this thesis) or partial response and interrupted response (Kudo and Ohtsuki, 1998; McGarry and Franks, 2003) are applicable to real-world full-body movements.

5.3. Practical implications

(i) Potential for perceptual training

In Chapter 3, we demonstrated that cognitive processes for speed discrimination and decision making of movement onset are critical factors for temporal accuracy in rapid interceptive action. To enhance the accuracy of speed discrimination and TTC estimation, there seems to be two approaches. One is improving the motor aspect. By shortening the minimum swing duration or timing the hitting later, batters could obtain a longer time for the cognitive process. Another approach is improving the cognitive aspect. By shortening or enhancing the accuracy of the cognitive process, batters could estimate the TTC and/or discriminate the ball speed with higher accuracy within the same time period. We presume that in many practical situations players might be eager to improve the first aspect but not the second aspect, which we think would play a key role in visual skills even at high-level competition. Actually, a recent study has reported that a perceptual-learning program improved elite baseball batters' vision and resulted in an improved offensive performance in an actual baseball game (Deveau et al., 2014). Thus,

we believe that there would be a potential benefit for perceptual training.

(ii) ***Proper cognitive preparation in baseball hitting***

Our results from Chapter 4 provide an important suggestion for cognitive preparation in actual baseball hitting. The investigation in Chapter 4 revealed that pre-activation of motor process before speed discrimination of target speed is necessary for the circumvention of the severe time constraints in the decision making of movement onset. Specifically, if batters intend to hit both fast- and slow-speed balls, they have to prepare for a fast-speed ball and withhold the swing initiation in case the ball speed is slower than anticipated.

However, many baseball coaches would instruct a player to discriminate the ball speed and then decide the swing onset according to the ball speed. If batters intend to do so seriously, there would be not sufficient time for speed discrimination at high-level competition and batters could not achieve successful control of movement onset. In the worst case, batters are scolded for an inappropriate swing start and this situation would increasingly make proactive preparation and inhibitory-control difficult. Thus, batters should be instructed to prepare for the potentially fastest ball speed and adjust to a slower ball speed using the inhibitory control. Moreover, when there is not enough time for speed discrimination even if batters properly employ inhibitory control, batters have to read the game situation and concentrate on one target speed. Being able to prepare for one target speed despite the existence of other target speeds might also be an important cognitive skill.

5.4. Thesis Conclusion

In summary, we found that in rapid interceptive actions, time-dependent

onset control increases the temporal accuracy more than strategy which relies on continuous control. It was also suggested that the use of onset control under a severe time constraint is restricted by a limit of perceptual function. Moreover, onset control was achieved by continuous subthreshold modulation of excitability in the subcortical motor circuit, which circumvented the severe time constraint in the decision of movement onset.

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