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EFFECTS OF NUMERIC ORDER AND MODE OF MOTOR CONTROL ON SUBJECTIVE TIME

(主観的時間感覚に与える数字の順番や運動制御モードの影響)

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Contents

The studies in Chapter 3 and Chapter 4 were published as below.

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Chapter 4: Herai, T. and Mogi, K., (2014), "Perception of temporal duration affected by automatic and controlled movements. ", *Consciousness and Cognition*, 29, 23–35

Abstract

The processing of temporal information is ubiquitous in cortical computation. It is important for both perception and action, serving as an essential element of how the brain constructs models of the environment. This thesis investigated effects of perceptual and motor contexts on subjective time empirically. The thesis is composed of five chapters.

In chapter 1, a motivation and a purpose of a research about subjective time were described. In chapter 2, review of preceding studies on subjective time was described. The following chapter 3 and 4 are the descriptions of experiments that I conducted.

In chapter 3, an effect of numeric order on time perception was investigated. Preceding studies suggested that magnitude of stimulus (e.g., physical size, brightness, digit, etc.) affected temporal processing of the brain. A subject perceived a stimulus with larger magnitude as longer than that with smaller magnitude. The presented stimuli that many preceding studies used were static. In this chapter, I investigated whether stimuli the magnitude of which changed gradually would also affect subjective time. The Arabic number, which is thought to be familiar to many people in Japan, was used as the stimulus. In the experiment, nine digits from '1' to '9' were presented in ascending, descending, or random order. A square followed the presentation of digits as a target stimulus. A presented interval of each digit was fixed at 500 ms. The target stimulus was presented shorter or longer than the each digit. A subject judged whether the presented interval of target was shorter or longer than that of each digit. The result showed that the subject tended to overestimate the target duration in ascending order condition compared to the other conditions. A point of subjective equality (PSE), which indicates the target interval that the subject perceived the target as the same duration as each digit, was calculated for each condition. The result of PSE showed that PSE in ascending order condition was significantly smaller than in descending order condition, indicating the subject perceived the target in ascending order condition as longer than in descending order condition. These results indicated that the stimulus the magnitude of which changes gradually also affected our temporal processing.

In chapter 4, an effect of mode of motor control on subjective duration was investigated. Sensorimotor contingency is one of the main factors to warp time perception. Preceding studies showed that voluntary actions such as saccades and hand movements affected the subjective perception of temporal duration. Motor control can be categorized hierarchically depending on an engagement of consciousness. For example, voluntary movement and intended action are thought to be close to conscious movement. On the contrary, reflex like movement and reflex are thought to be close to unconscious movement. In addition, spontaneous or self-timed movements are thought to be located intermediate between them. The preceding study showed that the perceived timings of action and stimulus are affected by whether an action was automatic or controlled. In this chapter, I investigated an effect of the mode of motor control on duration estimation. In the experiment, a duration reproduction paradigm was used. A subject remembered a reference interval and reproduced its length by keeping pressing a key after a Go signal. By limiting a timing at which the subject began to press the key after the Go signal, the mode of motor control was controlled. In experiment 1, an effect of automatic, self-timed, and cognitively controlled movement on reproduced interval was investigated. Reproduced intervals were shorter when actions were initiated by automatic manner, compared to self-timed or cognitively controlled actions. In experiment 1, the subjects knew which action they would conduct when they remembered the reference interval. Therefore, there was a possibility that an internal state such as attention and concentration were different between the conditions and it affected a process of remembering the reference interval. In experiment 2, the experimental procedure was modified so that the subject did not know which action she or he would do when remembering the interval of the reference stimulus. The result in experiment 2 was consistent with that in experiment 1. These results indicated that the mode of motor control affected our temporal processing in such a manner that automatic action might accelerate the flow of subjective time.

In chapter 5, general discussion was described. I summarized and discussed the results of the experiments in chapter 3 and 4. Future works were also given in this chapter.

In summary, this thesis showed that both perceptual and motor contexts affected our temporal processing. In both experiments in chapter 3 and 4, the factors that affected temporal processing were

set just before the subject estimated the interval. It was the order of digit and the mode of motor control in chapter 3 and 4, respectively. Therefore, it indicated that our subjective time progresses by being affected by both the context of perception and motor mechanisms.

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Chapter 1

Introduction

Our subjective time varies depending on a situation. For example, when we have fun, time flies. On the contrary, we feel time proceeding slower than usual when we are bored. There have been many reports that time slowed down when people met with a critical situation such as a traffic accident. Our subjective experience of time has also affected by ages (Lemlich, 1975). Many people say that the older they become, the faster they feel time progress. In a case of travel, we feel it take more time in the way to a destination than its way back. In a stressful situation such as making a speech in front of many people or going to a job interview, it seems that the subjective sense of time changes dynamically. When the speech proceeds smoothly, we notice time has passed in a moment. On the contrary, when forgetting the content of speech or not being able to answer a question, it seems like time freezes suddenly and moves slowly.

As just described, there are a lot of cases where subjective time changes in real life. However, the mechanism how the brain constructs subjective time is still unclear. A lot of researchers have investigated the mechanism of subjective time so far. Recently, thanks to the brain imaging technology, a lot of evidences about the mechanism of subjective time have been accumulated.

It is considered that subjective time has various aspects. We can detect temporal order of more than two events. As a delay between successive events decreases, a judgment which event happened first becomes difficult and then we perceive multiple events happening simultaneously. The threshold interval that we can detect temporal order of successive events was about 30 to 40 ms (Pöppel, 1988). This threshold was equal across modalities such as vision, audition, and touch. Even though we cannot say temporal order of these events explicitly under this threshold interval, there is a case where we can judge if they happened simultaneously or not.

We can also estimate temporal duration explicitly and implicitly. When playing a musical instrument, a player may bring her attention to a length of sound. In this case, the interval is estimated explicitly. On the other hand, when waiting for a traffic light or a train passage at railroad crossing, we occasionally happen to notice that it has taken long time since we began to wait. In this situation, it is considered that the temporal duration is estimated implicitly and compared with a stored interval in memory. Then, if the interval at the time is longer than the interval we have experienced in a similar situation, we make a judgment and feel that it has taken long time. In addition, when we cross a street, we estimate an interval that a car in the distance comes to us. It is what is called time-to-collision or time-to-contact (Tresilian, 1995). In this case, we expect the interval that will happen in the future and it may need a mechanism that solves the problem of time-to-collision.

A sensory organ that detects progress of time has not been found so far. However, taking its ubiquity and fundamental aspects into account, it is considered that there may be some basic mechanisms or processes that contribute to constructing subjective time in the brain. Therefore, it is thought that investigating the mechanism of subjective time will contribute to understand the basic mechanism of neural processing in the brain.

When we interact with our environment, both perceptual and motor systems of the brain are engaged. Both of them have temporal aspects such as duration and timing. One of the factors that sensorimotor integration goes well is whether temporal aspect of them is organized properly in the brain. Therefore, it is important to investigate the mechanism of temporal processing of both perception and action.

In this thesis, I reviewed preceding studies about subjective time in Chapter 2. Then I gave a description of experiments that I conducted to investigate effects of perceptual context and motor context on subjective time in Chapter 3 and 4, respectively. In Chapter 3, I investigated how order of number (e.g., ascending or descending) affected temporal processing of a stimulus that followed. In Chapter 4, I conducted the experiment which investigated an effect of mode of motor control at initiation of movement on subjective time. In Chapter 5, I summarized and discussed results of experiments in Chapter 3 and 4. Future works were also given in Chapter 5.

Chapter 2

Review of Preceding Studies on Subjective Time

2.1 Experimental Studies of Subjective Time

Recently, time perception ranging from sub-second to several seconds has been extensively studied. When a successive presentation of identical stimuli was followed by an oddball stimulus, a subject perceived the oddball stimulus as longer than the previous stimuli (oddball effect, Tse *et al*., 2004) (Figure 2.1).

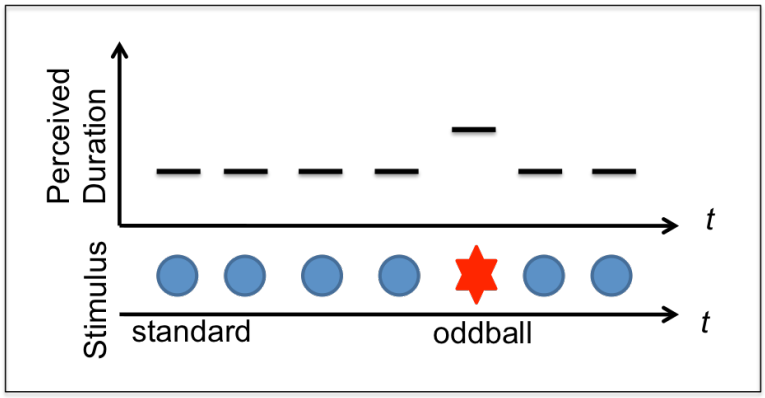


Figure. 2.1 Oddball effect. After a standard stimulus (a blue circle) is presented for several times, an oddball stimulus (a red star) is presented. A subject perceives the oddball stimulus as longer than the standard stimulus.

An onset of visual stimulus expanded the subjective time (Kanai & Watanabe, 2006). When the same stimulus was presented successively for several times, the first one was perceived as longer than the others (debut effect, Pariyadath & Eagleman, 2007). The debut effect disappeared when following stimuli were images that the subject was not able to predict such as a sequence of random digits. When the subject was able to predict the next stimulus, its perceived duration was shorter than when

she or he was not able to predict the next stimulus. Even though intervals of stimulus presentation were a few ten milliseconds, this effect was also observed (Pariyadath & Eagleman, 2008). It indicated that processing at early stage in the brain also had a role in constructing our subjective duration. The magnitude of the oddball effect was affected by repeated times of presentation of the same stimulus before the presentation of an oddball stimulus (Pariyadath & Eagleman, 2012). The difference of stimulus property such as an angle of a bar between a standard and an oddball stimuli also affected perceived duration (Pariyadath & Eagleman, 2012; Schindel *et al*., 2011). These results indicated that a saliency of stimulus was one of the key factors that affects subjective time. By spatially separating an oddball and a target stimulus, New and Scholl (2009) showed that the temporal dilation effect by an oddball was not spatially restricted to an area where the oddball was presented but it occurred at an entire visual field. Using fMRI, Wittmann *et al*. (2010) found that left medial frontal, the posterior cingulate and pre-cuneus rigions activated when the subjective duration expanded.

From a similarity between the pattern of the oddball effect and a repetition suppression of neural response, Eagleman and Pariyadath (2009) suggested that our perceived duration corresponds to a magnitude of neural responses to a stimulus. The repetition suppression is a phenomenon that neural responses decrease gradually as the same stimulus is presented repeatedly (Grill-Spector *et al*., 2006; Henson & Rugg, 2003). Their hypothesis is able to give an explanation to various illusions about subjective time.

Our perceived duration is also affected by a modality that processes a stimulus. Even though the same interval of a visual or an auditory stimulus was presented, a subject perceived the auditory stimulus as longer than the visual stimulus (Wearden *et al*., 1998). In addition, studies showed an effect of interaction between vision and audition on subjective duration. Using a multisensory oddball paradigm, van Wassenhove *et al*. (2008) found that visual stimulus affected perceived duration of auditory stimulus but the reverse pattern was rarely observed. On the contrary, Chen and Yeh (2009) showed that auditory modality affected temporal processing of visual modality but visual modality did not influence that of auditory modality. Disruption on processing by transcranial magnetic stimulation (TMS) also showed an asymmetric effect between auditory and visual modality (Kanai *et*

al., 2011). TMS over the primary auditory cortex impaired both auditory and visual temporal processing, while TMS over the primary visual cortex disrupted only visual temporal processing.

Furthermore, studies of audiovisual integration tell us how the brain constructs temporal representation such as perceived timing across modalities. For example, the transmission speeds of sound and light in the air are different. In addition, the conductance speeds from each sensory organ to the brain are different between them. Therefore, even though sensory stimuli are originated from the same event, arrival timings of them to the brain will be different across modalities. The brain has to deal with these differences of arrival times. A study showed that the brain compensate the delay between modalities to perceive simultaneously the event that actually happened the same time (Kopinska & Harris, 2004).

However, it is not fixed that how the brain compensates this delay. Fujisaki *et al*. (2004) showed that an adaptation to audio-visual time lag changed a delay between auditory and visual stimuli to be judged simultaneous. Furthermore, there is a temporal window in which stimuli of different modalities such as audition and vision are perceived simultaneously. This temporal window of simultaneity was widened when a subject were watching audiovisual asynchronous movie (Navarra *et al*., 2005). These studies suggested that the mechanism of constructing subjective time is not fixed from birth but dynamically changed by learning and knowledge.

Emotion is also one of the factors that affect our subjective time (Droit-Volet & Meck, 2007). Images that elicited fear were perceived longer than neutral images (Grommet *et al*., 2011). Perceived duration of emotional sound was longer than that of neutral ones (Noulhiane *et al*., 2007). Emotional negative image that a subject could not perceive consciously also lengthened perceived duration (Yamada & Kawabe, 2011). A direction of gaze affected the subjective duration (Doi & Shinohara, 2009). Subject's mood elicited by movies affected subjective time (Droit-Volet *et al*., 2011). Attractive face affected perceived duration (Arantes *et al*. 2013).

However, whether an emotional stimulus such as an angry face prolonged subjective duration was depended on a kind of temporal judgment used in an experiment (Gil & Droit-Volet, 2011). They used five temporal judgment methods (bisection, generalization, verbal estimation, production and reproduction) to investigate an effect of angry faces on temporal processing compared to neutral ones.

They observed the subjective lengthened effect of angry faces when bisection, verbal estimation and production method were used. This result indicated that various different neural mechanisms play a role in temporal processing according to purposes. In addition, when a subject had a feeling of control for stimulus presentation, the subjective lengthening effect of emotional stimuli was diminished (Buetti & Lleras, 2012; Mereu & Lleras, 2013).

In order to investigate whether the speed of subjective time slows down in crisis situation, Stetson *et al*. (2007) had their subject experience a free fall from the height. The subjects estimated an interval from beginning of falling to touching a net before and after they experienced the free fall. Before the free fall, they watched other person perform the free fall and they estimated the interval of free fall by imagining they would experience the free fall from the height. After they fell, it was estimated from their memory of the free fall. The result showed that the estimated interval were longer after they fell than before they fell. It indicated that the flow of subjective time decreased during the free fall. However, their temporal resolution did not change between falling in the air and standing on the ground although their subjective time dilated during the fall.

Color also affects time perception. A presented interval of red color on a monitor was overestimated more than that of blue color (Shibasaki & Masataka, 2014). Furthermore, Katsuura *et al*. (2007) exposed a subject to blue or red light environments and asked her or him to produce intervals of 90 or 180 s by a stopwatch. The produced intervals for 180 s but not for 90 s were significantly shorter in red light than in blue light environment. Subjective reports of various feelings measured by visual analog scale were not significantly different between the conditions, indicating that unconscious mechanism engaged in temporal processing.

Coull *et al*. (2011) reviewed the brain regions which were activated when a subject conducted various temporal tasks. The commonly activated areas in temporal tasks were basal ganglia, supplementary motor area (SMA), cerebellum, and prefrontal cortex. Their roles in temporal processing were different depending on task requirements. Basal ganglia were activated by various temporal tasks. Especially, the putamen and the caudate nucleus were the main regions that were activated by temporal tasks. In motor timing tasks, lateral areas of basal ganglia such as the putamen

were activated (Figure 2.2 A). In perceptual tasks, medial areas of basal ganglia such as the caudate and globus pallidus were activated. SMA was also activated both motor and perceptual timing tasks (Figure 2.2 B). A neural activity in pre-SMA at temporal task was also found in a monkey study (Mita *et al*., 2009). A role of cerebellum in temporal processing was more implicit and automatic than other areas that were engaged in timing tasks (Figure 2.2 C). The right prefrontal cortex was considered to engage in monitoring temporal information and make a decision whether an interval a subject measuring at that moment was shorter or longer than a memorized interval.

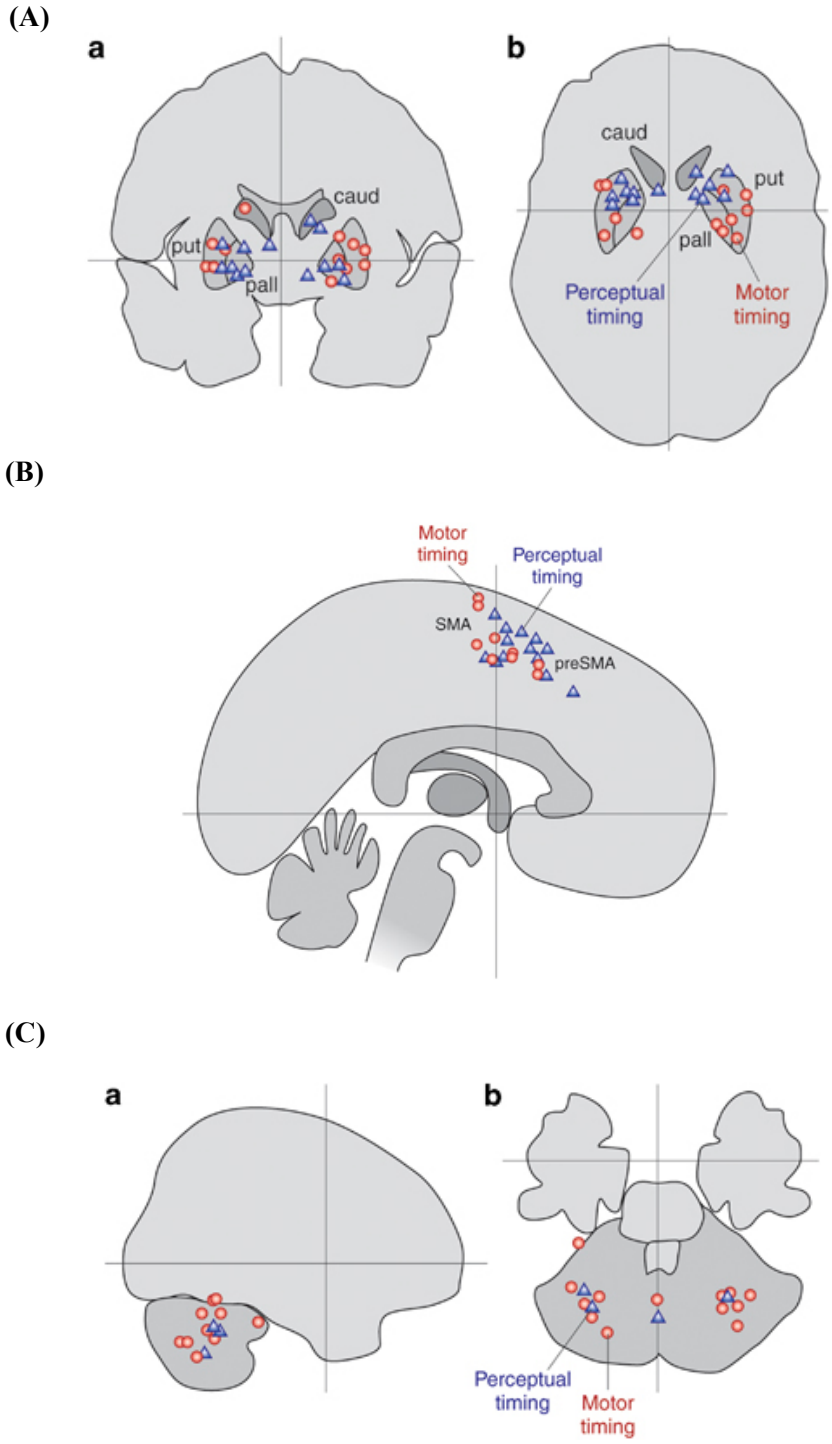


Figure 2.2 The brain regions which were activated by temporal tasks. **A**. The basal ganglia. (a) coronal view (b) transverse view. **B.** The supplementary motor area. **C.** The cerebellum. (a) lateral view (b) transverse view. Each mark indicates the area that was activated in various temporal tasks. Red circle and blue triangle represent that the task was about motor or perceptual timing, respectively. Adapted from Coull *et al*. (2011).

Subjective time is also affected by neurochemical substances. A level of dopamine is thought to modulate the speed of passage of time. Compared with a control condition, an injection of DA agonist (e.g., methamphetamine and cocaine) to rats shortened produced interval of a target interval, while an injection of DA antagonist (e.g., haloperidol or raclopride) lengthen it (Coull *et al*., 2011). This effect was also found in human subjects (Rammsayer, 1993). It is considered that higher dopamine level leads faster passage of time. In addition, acetylcholine is also related to subjective time and it plays a role in forming a memory of temporal information (Coull *et al*., 2011). A level of GABA concentration in visual cortex was correlated with individual differences of perceived duration of visual stimuli at interval discrimination task (Terhune *et al*., 2014).

As described above, the basal ganglia are found to be the one of the main regions that processes temporal information. It is thought that the effect of neurotransmitter on time perception is occurred in the basal ganglia. Figure 2.3 shows the neuropharmacological connections of the basal ganglia.

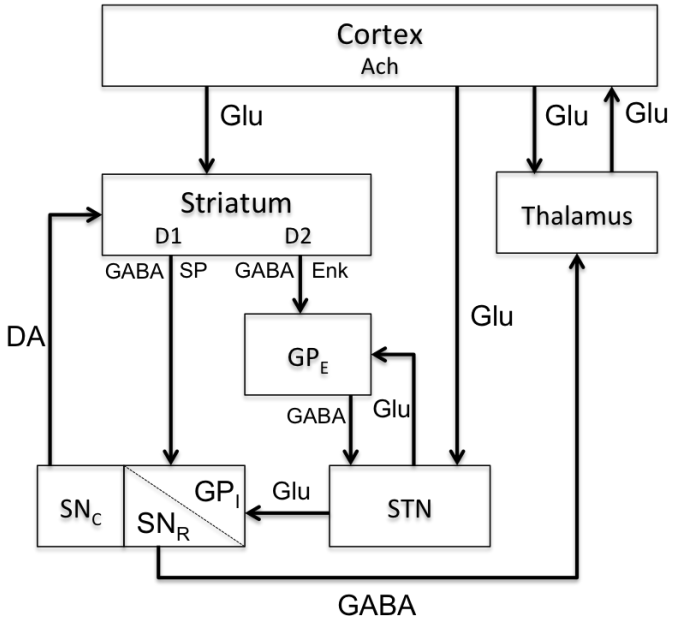


Figure 2.3 Neuropharmacological connections among the cortex, the basal ganglia, and thalamus. Abbreviations: Ach, acetylcholine; Glu, glutamate; GABA, gamma-aminobutyric acid; DA, dopamine; Enk, enkephalin; SP, substance P; D1, dopamine D1 receptor subtype; D2, dopamine D2 receptor subtype; GP_E, globus pallidus external capsule; GP_I, globus pallidus internal capsule; SN_C, substantia nigra pars compacta; SN_R, substantia nigra pars reticulata; STN, subthalamic nucleus. Adapted from Meck (1996).

As just described, various brain regions and neurochemical substances were found in the experiments about subjective time. For this reason, various neural models for temporal representation have been suggested (Ivry & Schlerf, 2008). Whether temporal information is processed by dedicated or intrinsic timing mechanism is one of the factors that categorize them. Dedicated timing models hypothesize that there are some neural structures specialized for processing temporal information across various temporal tasks. On the other hand, intrinsic timing models do not hypothesize an existence of something special neural brain structures which dedicate for processing of temporal information. Instead, it suggests that time is intrinsically represented in dynamics of neural activation such as spatial pattern.

2.2 Internal Clock Model

The pacemaker-accumulator internal clock model has been developed to account for interval estimation (Treisman, 1963). One of the applications of the model is the Scalar Expectancy Theory (SET, Gibbon, 1977; Gibbon *et al*., 1984). In SET, there are three stages (clock, memory and decision), each stage containing a few components (Figure 2.4). In the clock stage, it is assumed that there is an internal clock which emits pulses with a certain rate. Those pulses then pass a gate of accumulator. The gate is open by default. When the cognitive process of estimating intervals is initiated, the switch of the gate is closed and pulses are accumulated. The interval is then measured by the amount of pulses in the accumulator. The working memory of the amount of pulses or the estimated duration of interval is held at the memory stage. This memory will be processed further and stored in a reference memory for later comparisons of intervals. A comparison of reference memory with a new progressive interval is conducted at the decision stage. In this last stage of SET, the online estimation of the new interval in working memory is compared with the stored interval in the reference memory. Based on this process, the subject makes judgments about the duration and timing.

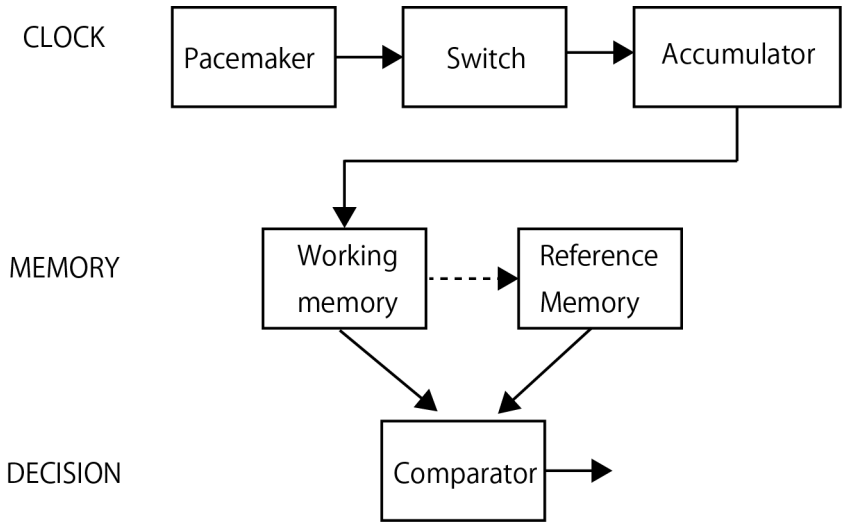


Figure 2.4 A schematic diagram of SET internal clock model. Adapted from Yarrow *et al*. (2004a).

One of the predictions of the SET is the scalar property of variance: The distribution of estimated interval would scale in proportion to the mean of estimated interval, so that the coefficient of variation (the standard deviation divided by the mean) is constant, as the estimated interval changes.

A model incorporating an internal clock in general indicates that the clock rate and the latency of the closing and opening of the switch are the critical factors for estimating interval. Variations in those components would affect the temporal estimation differently. While a change in the clock rate would result in a proportional effect for the interval, a change in the timing of switch closing or opening would lead to a constant shifting effect in the perceived interval.

The discrepancy between objective and subjective time can be explained by the change of clock rate. Figure 2.5 shows an example that how the change of clock rate affects perception of temporal duration. One of the factors affecting the clock rate is arousal. It has been suggested that a higher arousal level correlates with a faster clock rate. A click train might increase the arousal level, resulting in an overestimation for the following intervals (Penton-Voak *et al*., 1996).

The studies showed that supplementary motor area (SMA) is a candidate brain region where the process of pulse accumulation occurs (Coull *et al*., 2011). Basal ganglia are thought to encode duration (Coull *et al*., 2011).

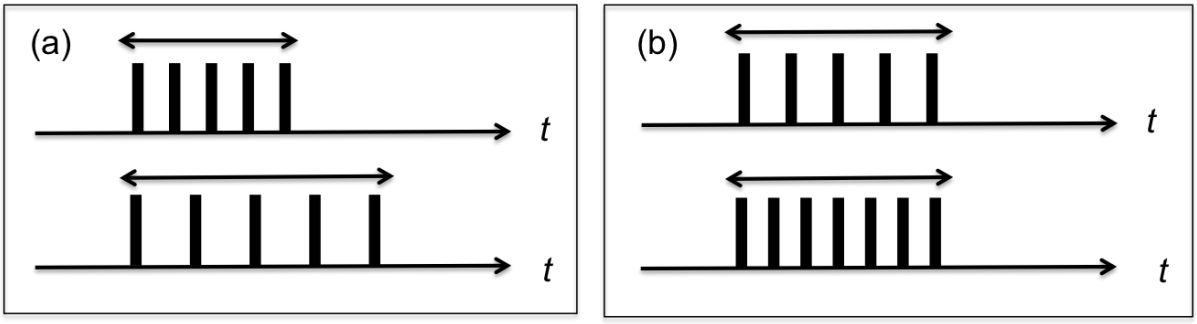


Figure 2.5 An example of discrepancy between objective and subjective duration explained by number of pulses. An axis indicates the flow of objective time and a range of two-headed arrow indicates an actual interval of stimulus presentation that a subject estimates. Rectangle on the axis indicates a pulse the internal clock emits. (a) Although the actual durations at top and bottom axes are different, the subject perceives both intervals equally because the numbers of pulses contained are the same. (b) The subject perceived the interval at top axis as shorter than at bottom axis, though their intervals are actually equal. This is because the number of pulses at bottom axis is more than in top axis.

Chapter 3

Effect of Numeric Order on Subjective Time

3.1 Introduction

Studies have showed that a property of stimulus itself affects our perceived duration. Non temporal factors such as spatial size and magnitude of stimulus also affect its perceived subjective duration. A presented duration of larger stimulus was estimated to be longer than that of a smaller one (Rammsayer & Verner, 2014; Xuan *et al*., 2007)(Figure 3.1). This effect also occurred with more conceptual stimuli such as numbers (Chang *et al*., 2011; Oliveri *et al*., 2008; Vicario *et al*., 2008; Vicario, 2011). The effect of number on subjective time was influenced by type of weight unit bound to presented digit (Lu *et al*., 2009). Words which implicitly represent magnitude of various non temporal dimensions (e.g., length, weight, and volume) also affected our temporal processing (Ma *et al*., 2012). These studies suggested that higher mechanism might involve an interaction between subjective time and various dimensions.

A theory of magnitude (ATOM) hypothesizes various dimensions such as space, time, and quantity are represented by a similar or a common neural mechanism (Walsh, 2003). ATOM suggests that these dimensions interact each other and it results in that the magnitude of one dimension affects the other dimensions. Studies showed that parietal cortex is the brain area where this common metric mechanism might exist (Bueti & Walsh, 2009; Walsh, 2003) (Figure 3.2). For the magnitude of number, the horizontal segment of intraparietal sulcus was activated irrespective of whether a notation was Arabic digits or dot patterns (Piazza *et al*., 2007). It suggested that the magnitude of number was coded abstractly.

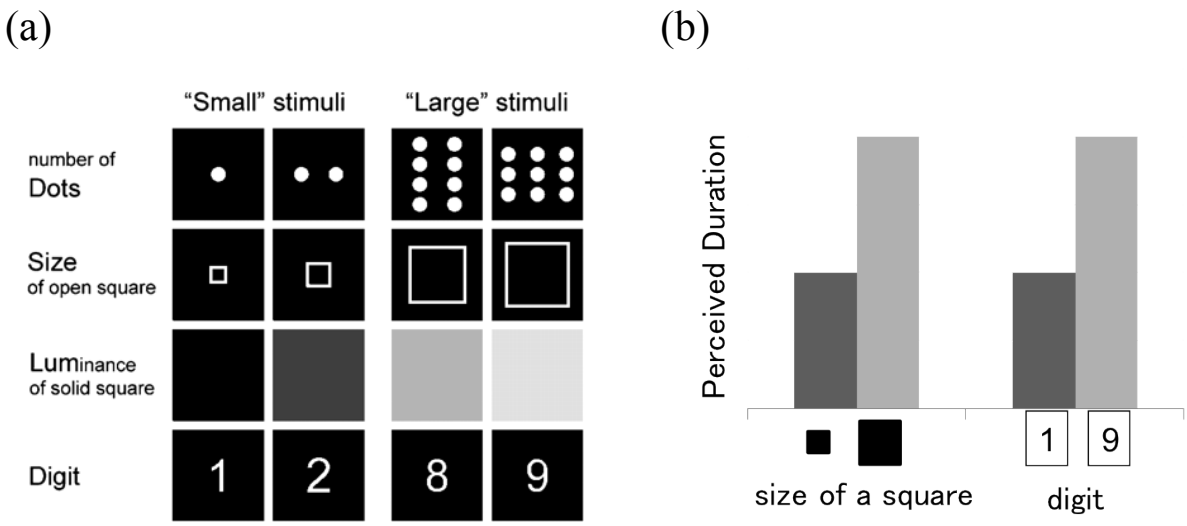


Figure 3.1 (a) Example of stimuli that have "small" and "large" magnitude. Adapted from Xuan *et al.* (2007). (b) A conceptual diagram of perceived duration of stimuli with small or large magnitude. A subject perceives "large" stimuli as longer than "small" stimuli. Note that not only physical size such as a size of a square but also an abstract stimulus such as Arabic number induces the effect.

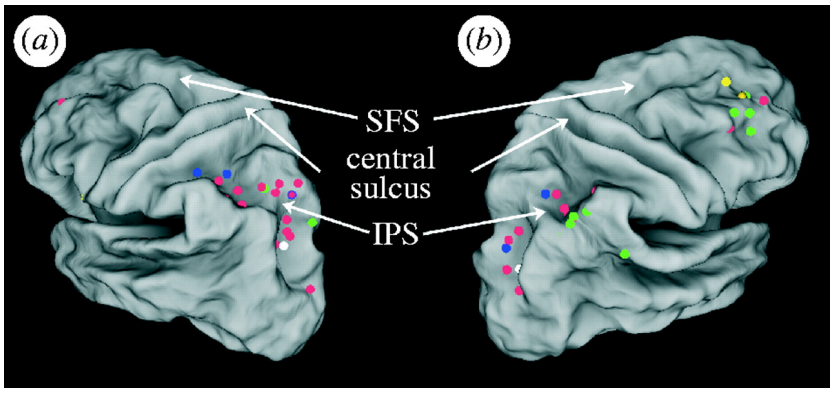


Figure 3.2 The brain regions which were activated by tasks related to various dimensions. (a) left and (b) right hemisphere of the visual cortex in human. Each point represents the dimension of magnitude used in the tasks (green = time; space = yellow; number = red; size = blue; white = luminance). Abbreviations: IPS, intraparietal sulcus; SFS, superior frontal sulcus. Adapted from Bueti and Walsh (2009).

In a real environment, there are many cases where a magnitude of stimulus changes continuously. For example, a size of object is becoming larger or smaller when it is approaching or receding to us, respectively. When viewing movie and listening to music, a volume of a sound becomes larger or smaller gradually as people try to change the level of volume. There is an illumination a brightness of which can be modulated by turning a knob and we can get an appropriate brightness for a situation by changing the magnitude of brightness.

For interacting with an environment appropriately, it is important to precisely detect whether a magnitude of sensory stimulus changes either increasingly or decreasingly. For instance, we can realize something is approaching when a sound becomes larger and larger.

Therefore, it is considered that there may be a mechanism which detects a direction of changes of magnitude of some dimension. Taking ATOM into account, I hypothesized that changes of magnitude of various dimensions interact and the direction of changes in one dimension affects the other dimensions. As well as ATOM, one of such magnitude might be subjective time. So, I conducted the experiment which investigated an effect of changes of non temporal magnitude on subjective time. If such effect is found, the framework of ATOM will be extended to include a continuous changes of magnitude.

Especially, among various dimensions, it is thought that numbers are often used in a real life as counting up and counting down. People often count up numbers for detecting how many things there are and how many times they have done something such as push-ups. We usually count down numbers when something will be completed or start such as a rocket launching.

In recent years, digital devices (e.g., a personal computer, a tablet, and a smartphone) are used widely. Variety of information, such as sound volume, buttery, time, and processing of file copying/downloading, is displayed with numbers on these devices and values of them change continuously in many cases. Therefore, we are familiar with continuous changes of visually displayed numbers in a life. There is a possibility that these changes of numbers affect our subjective time. In the experiment in this chapter, I investigated the effect of order of numbers (ascending or descending) on time perception.

Our introspection is different between the ascending and the declining numbers. The ascending numbers may be categorized to a representation like as “up” and “expansion”, while the declining numbers may be categorized to a representation like as “down” and “contraction”. I hypothesized that the magnitude of the former may be perceptually categorized as larger than that of the latter and this difference of magnitude would affect our time perception as ATOM supposes. I predicted that the ascending numbers would induce temporal lengthening effect and it would affect subjective duration on a stimulus presented just after numbers.

3.2 Methods

3.2.1 Experiment 1

Nine subjects (8 naïve [3 female] and author T.H, mean ± s.d age = 28 ± 2.4) participated in the experiment 1. They have normal or corrected-to-normal vision. Informed consent was obtained from all participants. Stimulus presentation and collecting of subject’s response were controlled by a PC (Panasonic CF-W4). Visual stimuli were presented on a 17-inch monitor (Eizo FlexScan S1911/S1922) with a refresh rate of 60 Hz. One of nine white digits (from ‘1’ to ‘9’ [0.04°in width and 0.07° in height]) and a white square (0.06°) were presented at the center of the monitor with a black background. Subjects sat in front of the monitor at the distance of 60 cm with a chin rest.

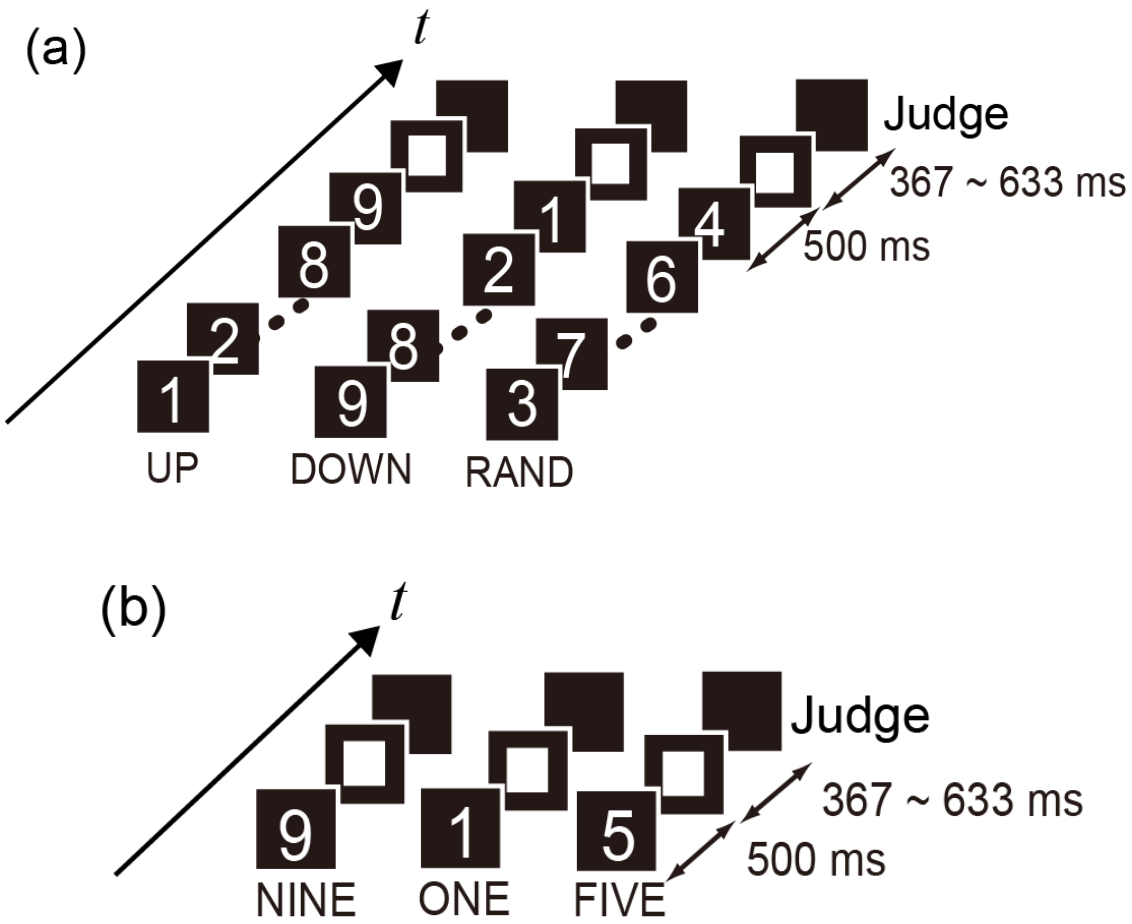


Figure 3.3 Experimental procedures in experiment 1 (a) sequential numbers condition (b) single number condition. In sequential numbers condition, a total of nine integers from one to nine were presented before a target stimulus (a white square). The order of digits was ascending and descending in the UP and the DOWN condition, respectively. In the RAND condition, the order of digits was randomized. In single number condition, only one digit was presented before the target stimulus. The presented digits were '9' in the NINE and '1' in the ONE condition and they corresponds to the last digit in the UP and the DOWN condition, respectively. In the FIVE condition, the presented digit was '5'. The subject judged whether the temporal duration of the target was longer or shorter than that of each digit.

The experiment consisted of a sequential numbers condition and a single number condition (Figure 3.3). In the sequential numbers condition, each of numeric stimuli was presented successively with a standard duration (500 ms). Subjects were instructed beforehand that the presented duration of each digit was equal. There were three types (UP, DOWN and RAND) of order in digits presentation. In

the UP condition, each number appeared in ascending order, while number goes down in order in the DOWN condition. In the RAND condition, the presented order of digits was randomized. Therefore, in this condition subjects were not able to predict the next number. The RAND condition was included for enhancing the subject's attention to the order of digits, by making the ascending and descending order salient. The RAND condition was also designed to avoid the subjects suspecting the aim of experiment.

After the last digit was presented, the white square was presented with one of nine durations (367, 400, 433, 467, 500, 533, 567, 600, and 633 ms). No delay was inserted within successive digits and between the last digit and the target. After the stimulus presentation, participants judged whether the duration of the last square was longer or shorter than that of each of numeric stimuli and responded by pressing the button of mouse with their right hand.

Three types of number presentation were mixed randomly in one block. Each of test durations was presented once for each of conditions in a block. Therefore, each block contained 27 trials (9 durations × 3 conditions). Subjects conducted a total of 10 blocks.

Furthermore, to investigate whether there was any effect of the last digit to the duration estimation, I conducted the single number condition. Experimental setting was the same as the sequential numbers condition except that only one of three digits ('9', '1', or '5', NINE, ONE or FIVE condition, respectively) was presented as a reference stimulus for 500 ms before the target appeared with valuable delays. The '9' and '1' were the last digits in the UP and in the DOWN condition, respectively. In the FIVE condition, the presented digit was ‘5’ and its magnitude was considered intermediate among all digits that used in the experiment. Ten blocks were conducted in each condition. The sequential and single number conditions were changed by five blocks and the order of them was counterbalanced among the subjects.

3.2.2 Experiment 2

In experiment 1, the order of number presentation influenced the temporal processing of following stimulus. In the sequential numbers condition of experiment 1, the last digit before the target stimulus was different. The results of the single number condition indicated that the overestimation of the

target duration in the UP than in the DOWN condition was not caused by the digit before the target. However, in order to reduce the difference of the conditions, I conducted the experiment in which the digit before the target was the same among the order of digit presentation. I predicted that, as well as experiment 1, when the order of digits would be ascending, the subject would overestimate the target duration more than when the digits were presented in the descending order.

Eight subjects (7 naïve [3 female] and author T.H, mean ± s.d, age = 28 ± 2.4) participated in experiment 2. They have normal or corrected-to-normal vision. Informed consent was obtained from all participants. The experiment was controlled on a desktop PC (EPSON Endeavor). Visual stimuli were presented at the center of a 21-inch CRT monitor (Sony, Trinitron, CPD-G520) with a refresh rate of 100 Hz. One of nine white digits ('1' to '9' [0.05° in width and 0.08 in height]) and a white rectangle (0.04° in width and 0.08 in height) were presented in a black background. Unlike experiment 1 in which the target was the square, I used the rectangle as the target stimulus in order to decrease the difference of physical size between the digit and the target. This modification would reduce the saliency of the target and weaken the oddball effect. Subjects sat in front of the monitor at the distance of 60 cm with a chin rest.

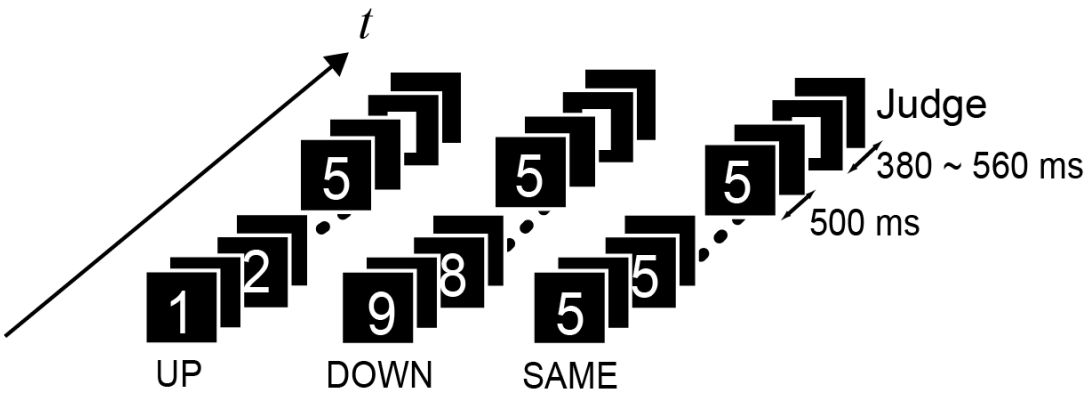


Figure 3.4 Experimental procedures in experiment 2. There were three conditions. Total of five digits was presented before the target stimulus. In the UP condition, the digits were ascending from one to five. In the DOWN condition, the digits from five to nine were presented by descending order. The digit of '5' was presented five times in the SAME condition.

Figure 3.4 shows the experimental procedures. The total of five digits were presented in order before the presentation of the target stimulus. There were three conditions in number presentations (UP, DOWN, and SAME). The digits from '1' to '5'and from '9' to '5' were presented sequentially in the UP and the DOWN conditions, respectively. In the SAME condition, all of presented digits were '5'. The reason why I used the SAME condition, not the RAND condition, was for simplicity of experiment.

There were blank intervals between all digits. The blank interval was randomly chosen from 300, 350, 400, 450, 500 ms. I used the random interval to avoid the subjects using rhythmic information for temporal estimation. Each digit was presented 500 ms. The range of presentation interval of target stimulus was from 380 to 560 ms by 20 ms bin. The results in experiment 1 indicated that the subjects tended to overestimate the target duration in general. Most of their judgments were 'longer' when the presented intervals of target were 567, 600, and 633 ms. In order to focus on more sensitive areas of temporal judgments, the range of target intervals was changed to be shorter.

The subjects judged whether the target interval was longer or shorter than the presented interval of each digit. Three conditions were mixed and randomly presented in a block. The subject responded by pressing the button of mouse. The target interval for each condition was presented one time in one block. One block contained 27 trials. The subjects conducted 10 blocks all.

3.2.3 Data Analysis

Subject's responses were plotted as a function of the target durations. Using maximum likelihood estimation, the data for each subject for each condition were fitted to the Weibull function:

$$F(x;\alpha,\beta) = 1 - \exp\left\{-\left(\frac{x}{\alpha}\right)^{\beta}\right\} .$$

where F represents a proportion of 'long' responses. x is the target duration. α and β are fitting parameters. Fitting parameters for each subject were used to estimate their Point of Subjective Equality (PSE: 0.5 point of fitted responding curve) and Just Noticeable Difference (JND: a difference of estimated duration between 0.75 and 0.5 point). A PSE indicated a target interval where

the subjects perceived the target as the same duration with the interval of each digit. The smaller PSE became, the more the subject overestimated the duration of the target presentation (Figure 3.5). JND indicated sensitivity of temporal discrimination.

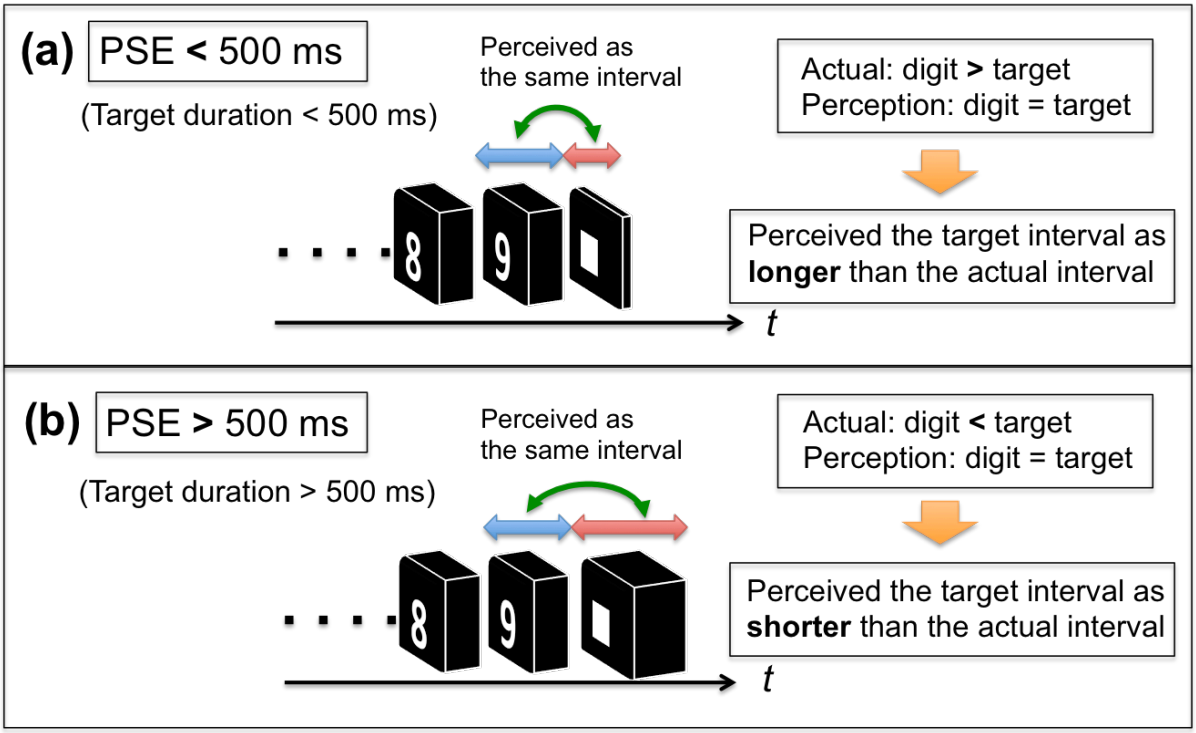


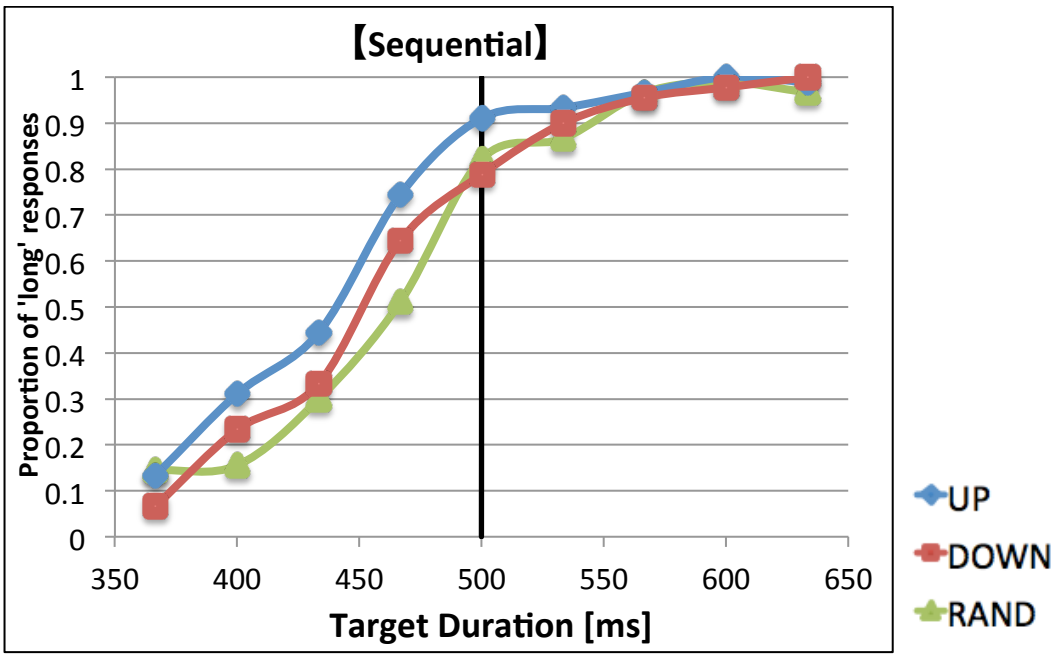
Figure 3.5 A relation between a value of PSE and perceived duration of the target stimulus. A thickness of a tile that represents each stimulus indicates an actual duration of a stimulus. The thinner the tile becomes, the shorter its presented interval becomes. (a) In case PSE is smaller than 500 ms. A subject perceived the target as the same interval as the digit, although the presented interval of the target was actually shorter than the digit. Therefore, the subject overestimated the target duration. (b) In case PSE is larger than 500 ms. The subject perceived the target as the same interval as the digit, though the target was presented longer than the digit actually. In this case, the subject underestimated the target duration. Therefore, the smaller PSE becomes, the longer the subject perceived the target duration.

3.3 Result

3.3.1 Experiment 1

Figure 3.6 shows the mean proportion of 'long' responses plotted as a function of the target durations in each condition. The responses of the sequential numbers and the single number conditions were submitted separately to two-way within-subjects ANOVA. The one of the factors were the target intervals. The other factor was the order of numbers (the sequential numbers condition) or the number presented before the target (the single number condition). The effect of the target intervals was significant both in the sequential numbers ($F(8, 64) = 146.37$, $p < 0.001$) and the single number ($F(8, 64) = 58.53$, $p < 0.001$) conditions. The effect of present order of numbers was significant in the sequential numbers condition ($F(2, 16) = 6.19$, $p = 0.010$). On the other hand, in the single number condition, the effect of the number before the target was not significant ($F(2, 16) = 0.61$, $p = 0.57$). The interaction was not significant in the sequential numbers condition ($F(16, 128) = 1.65$, $p = 0.065$) nor the single number condition ($F(16, 128) = 1.09$, $p = 0.37$).

(a)



(b)

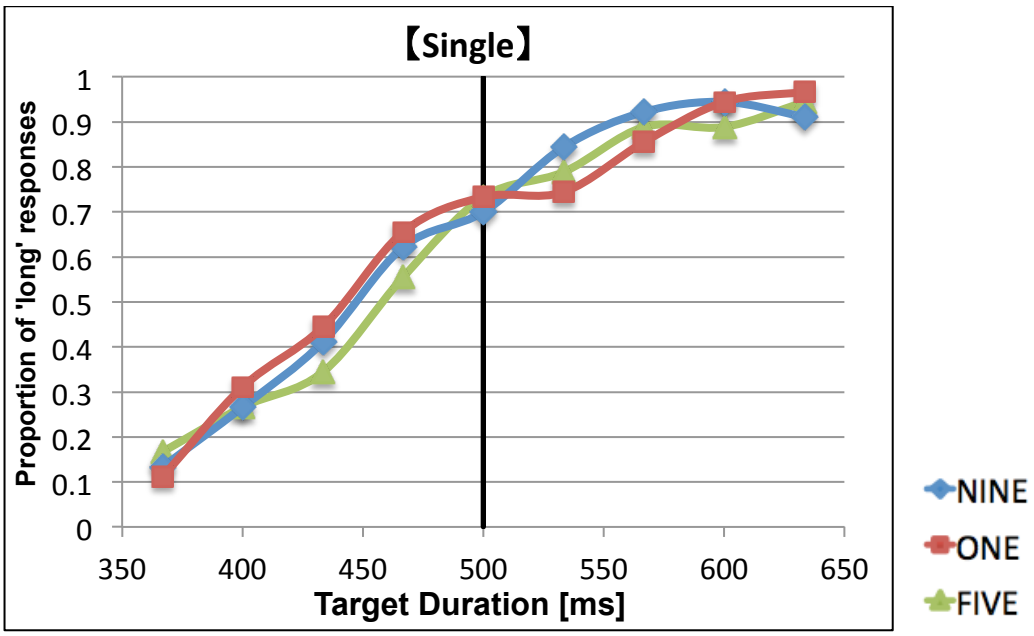


Figure 3.6 Proportion of 'long' responses in experiment 1. (a) sequential numbers condition (b) single number condition. A vertical line at 500 ms indicates the presented duration of each digit (i.e., the presented duration of target stimulus was the same as that of each digit).

Figure 3.7 shows the mean PSE for each condition. The values of mean and standard deviation of PSE and JND for each condition are shown in Table 3.1. In the sequential numbers condition, PSEs of

all conditions were significantly different from 500 ms (UP: $t(8) = -5.22$, $p < 0.001$, DOWN: $t(8) = -5.49$, $p < 0.001$, RAND: $t(8) = -2.56$, $p = 0.033$). In the single number condition, only ONE condition was significantly different from 500ms (NINE: $t(8) = -2.08$, $p = 0.070$, ONE: $t(8) = -2.35$, $p = 0.046$, FIVE: $t(8) = -2.07$, $p = 0.071$). A priori hypothesis that the ascending order would induce overestimation of the target interval more than the descending order was tested by a paired t-test. The difference of PSE between the UP and the DOWN condition was significant (paired t-test, $t(8) = -2.37$ $p = 0.044$) but between the ONE and the NINE was not (paired t-test, $t(8) = 0.34$, $p = 0.73$). Therefore, the subjects overestimated the duration of target stimulus more in the UP than in the DOWN condition and this difference might not be attributed to the digit just before the target. The JNDs were not different significantly in both pairs (paired t-test, UP vs DOWN: $t(8) = 0.12$, $p = 0.90$, ONE vs NINE: $t(8) = -0.68$, $p = 0.51$).

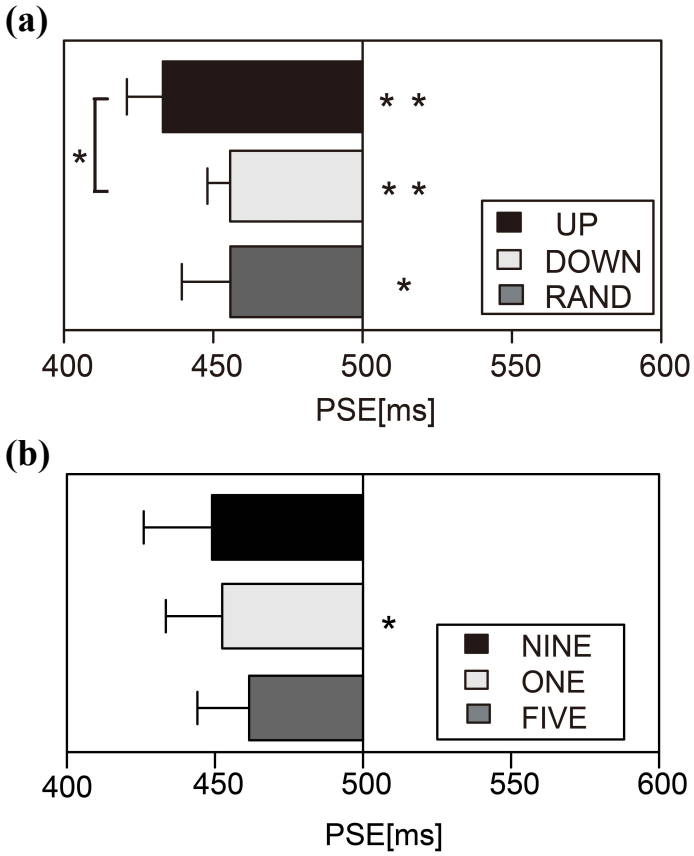


Figure 3.7 Mean of point of subjective equality (PSE) in experiment 1 (a) sequential numbers condition (b) single number condition. Error bar indicates standard error. * p<0.05, **p<0.01

Table 3.1 Mean of point of subjective equality (PSE) and just noticeable difference (JND) in experiment 1. The numbers in parentheses are standard deviations.

	Sequential Numbers			Single Number		
	UP	DOWN	RAND	NINE	ONE	FIVE
PSE	433 (36)	455 (22)	455 (48)	449 (69)	452 (57)	461 (52)
JND	42 (12)	41 (10)	46 (18)	62 (28)	57 (15)	59 (21)

3.3.2 Experiment 2

The data were analyzed as well as experiment 1. The results are shown in Figure 3.8. The proportion of 'long' responses was submitted to two-way within-subjects ANOVA. The factors were the target interval and the order of digits before the target. The effect of order of numbers was significant ($F(2,14) = 8.03$, $p < 0.01$). The target interval had also a significant effect ($F(8, 56) = 32.45$, $p < 0.001$). The interaction was not significant ($F(16, 112) = 1.02$, $p = 0.44$).

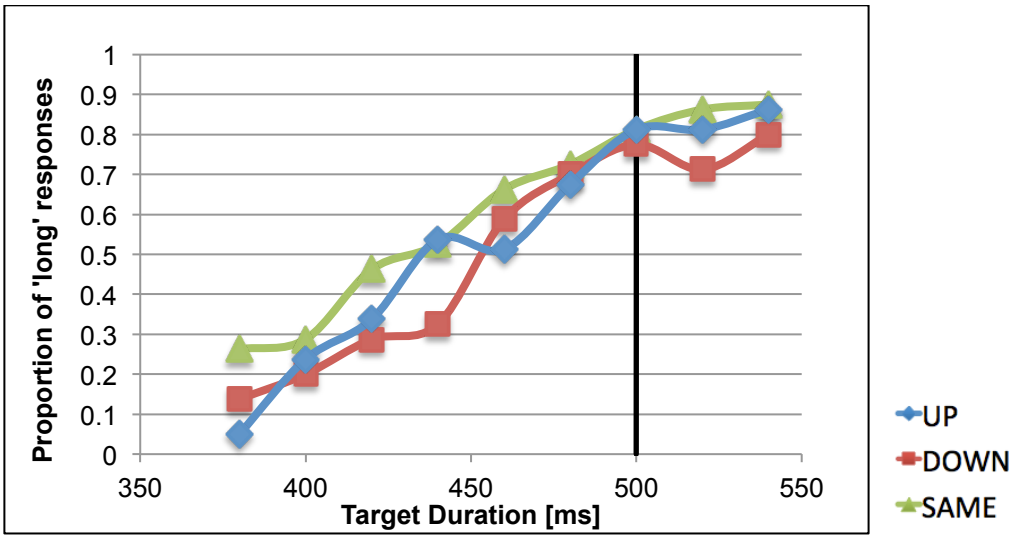


Figure 3.8 Proportion of 'long' responses in experiment 2. A vertical line at 500ms indicates the presented duration of each digit.

Figure 3.9 showed the mean PSE in experiment 2. The values of mean and standard deviation of PSE and JND in experiment 2 are shown in Table 3.2. The PSEs in all conditions were significantly

smaller than 500 ms (one sample t-test, UP: $t(7) = -5.00$, $p = 0.0015$, DOWN: $t(7) = -3.71$, $p = 0.0074$, SAME: $t(7) = -6.53$, $p = 0.00032$). As in experiment 1, the prior hypothesis that the ascending order would lengthen the perceived duration of the target stimulus more than the descending order was tested. Contrary to experiment 1, the difference of PSE between the UP and the DOWN was not significant ($t(7) = -0.49$, $p = 0.63$). JND was also not significantly different between the UP and the DOWN conditions ($t(7) = -1.61$, $p = 0.15$).

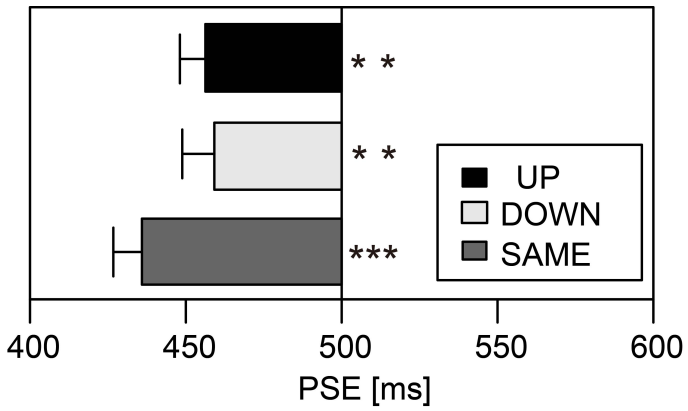


Figure 3.9 Mean of point of subjective equality (PSE) in experiment 2. Error bar indicate standard error. ** p<0.01, ***p<0.001

Table 3.2 Mean of point of subjective equality (PSE) and just noticeable difference (JND) in experiment 2. The numbers in parentheses are standard deviations.

	UP	DOWN	SAME
PSE	456 (23)	459 (29)	435 (25)
JND	45 (19)	62 (42)	54 (18)

3.4 Discussion

In this study, I examined whether temporal estimation was affected by the context just before the target. In experiment 1, when the digits were presented in the ascending order (UP), subject perceived the following square as longer in duration than in the descending order (DOWN). The non-significant

difference of JNDs between the UP and the DOWN conditions indicated that the subjects' sensitivities of temporal discrimination were not changed between these conditions. These results, in all, indicated that the preceding context affected the subsequent temporal processing in the brain.

Both the oddball (Tse *et al*., 2004) and the prediction (Pariyadath & Eagleman, 2007) effects might contribute to the subjects' altered temporal estimation in the present study. In the sequential numbers condition, the oddball effect always occurred because the visual property of the target stimulus was largely different from that of the digits. This effect expanded the perceived subjective duration of the target stimulus. At the same time, in the UP and the DOWN conditions, but not in the RAND condition, the subjects could predict the next digit, resulting in the perceived duration of the digits being contracted than actual. Therefore, in the UP and the DOWN conditions, the oddball and the prediction effects contributed to overestimate the target, while only the oddball effect did in the RAND condition. This suggestion is confirmed by the statistical analysis where the shifts of PSE from the standard duration (500 ms) in the UP and the DOWN conditions were more robust than that in the RAND condition.

In experiment 2, the proportion of 'longer' responses indicated that the perceived duration of target interval was overestimated more in the SAME condition than in the UP and the DOWN conditions. The transition of digit was lower in the SAME condition than in the UP and the DOWN conditions. Therefore, the saliency of target stimulus was higher in the SAME condition than in the UP and the DOWN conditions. So, the target stimulus might catch the subject's attention more in the SAME condition than in the UP and the DOWN conditions. Since attention affects the perceived interval (Mattes & Ulrich 1998), the subjects tended to overestimate the target interval more in the SAME condition than in the UP and the DOWN conditions.

In addition to these effects, the results indicated that the presented order of digits before the target stimulus affected subjects' temporal perception. The subjects tended to overestimate the target duration in the UP condition to a significantly larger extent than in the DOWN condition. The contextual effect of the digits order might be added to the oddball and prediction effects, resulting in smaller PSE in the UP condition than in the DOWN condition. I give below a few possible explanations why the order of digits affected the subject's temporal estimation.

The first possibility is that the subjects' expectation to the next stimulus, which was made by the pattern of digits order, affected the temporal estimation. In this case, the subjects expected that the next stimulus would be bigger (or smaller) than the previous one. So, they had larger (smaller) prediction when they watched the target stimuli in the UP (or the DOWN) condition. In the same manner as larger stimuli was perceived longer, this expectation also affected the processing of target stimulus and led to a more significant overestimation in the UP condition than in the DOWN condition.

Another possible account is to deal with the train of digit more comprehensively. The ascending (declining) number induced the internal representation of expansion (contraction) within the subject's brain, resulting in a differential processing of the target stimulus subsequently entered. The processing of the target stimulus might be affected by this brain state, changing the perceived subjective duration. When the target stimuli interacted with the brain state which represented either expansion or contraction, the target was consequently perceived as longer or shorter.

This internal brain state generated by the digits train may be also related to attentional state. Ascending numbers might draw up arousal level more than the declining numbers, resulting in the subjects attending to the stimuli more in the UP condition than in the DOWN condition. Since the attention expanded perceived duration (Mattes & Ulrich 1998; Tse *et al*., 2004), the subject could overestimate the target stimuli more in the UP condition as a result.

The studies showed that perception of numbers affected our various cognitive processes other than temporal processing. In the study of Badets *et al*. (2007), the subject judged whether she or he was able to grasp the lengthways of rectangle, which was presented on a monitor, between the thumb and index finger. Before the presentation of rectangle, a digit or a neutral symbol was presented. The digit was small ('2') or large ('8') magnitude. When the rectangle followed the small digit, the length the subject judged she or he could grasp became longer than when the large digit was presented. This result indicated that the magnitude of digit primed and affected evaluation of the lengthways of rectangle. The experimental paradigm was similar to the present experiment. The number was presented before the target stimulus that the subject judged its length or duration. However, in Badets *et al*. (2007) study, a single digits affected estimation of the lengthways of rectangle. In the single

digit condition of experiment 1 in the present study, the presentation of single digit did not affect perceived duration of the following stimulus, while the presentation of digit sequence did. A link between number and time might be different from a link between number and physical size.

Fischer *et al*. (2003) found that a mere presentation of single digit caused a shift of spatial attention. The direction of attentional shift was affected by the magnitude of digit. Small digit (‘1’ or ‘2’) induced the spatial attention to left space, while large digit (‘8’ or ‘9’) to right space. They suggested that this was caused by an interaction with mental number line. Mental number line indicates that small number is tied to left side of space and large number to right side of space (Hubbard *et al*., 2005). Furthermore, there were studies which showed our temporal processing was affected by left or right side of space (Vicario *et al*., 2008). The stimulus presented at right side was perceived as longer than when it was presented at left side. The shift of spatial attention to rightward (leftward) by prismatic adaptation induced overestimation (underestimation) of temporal duration compared with the performance before prismatic adaption (Frassinetti *et al*., 2009). Therefore, in the present study, the ascending and descending number might induce the shift of spatial attention to right side and left side of the space, respectively. These spatial shifts of attention may affect temporal processing of the target stimulus. However, it was still unclear why the single number condition did not induce the significant change of temporal processing of the target stimulus among the conditions.

The result can be explained by internal clock model. When the digits were presented in the ascending order, the clock speed accelerated gradually as the magnitude of number became larger. On the contrary, the clock speed slowed down gradually when the order of digits was descending. As a result, the clock speed at the time when the subject watched the target was faster in the ascending numbers than in the descending number. The number of pulses accumulated while presenting the target stimulus was larger in the ascending (UP) than in descending (DOWN) condition. Then, the subject's perceived duration of the target was longer in the UP than in the DOWN condition.

In the experiment 2, there was not the significant difference between the UP and the DOWN conditions. The presented number of digits before the target stimulus in experiment 2 was smaller than that in experiment 1. In addition, in experiment 2, there were blanks between each digit and the target. These differences of experimental paradigm might weaken the effect of context of digits order

on subjective time. It indicates that keeping the context of digits order to some extent may be necessary to induce the change of temporal processing which the experiment can measure.

ATOM suggests that various dimensions such as time, space, and quantity are processed by the common mechanism in the brain and magnitude of one dimension affects that of the other dimensions. I would propose that the present result might extend ATOM. The continuous changes of magnitude of various dimensions may be also processed by the common mechanism and interact each other. As I investigated only the number-time interaction in the present experiment, it needs to put other kind of interaction between different dimensions to the test to validate this proposal.

In summary, I showed that the order of numbers presented before the target stimulus affected the perceived subjective duration. When the integer presentation before the target was upward, the subjects overestimated the target duration larger than when the order was downward. The digits train before the target might induce different brain states, resulting in affected temporal processing of the target stimulus presented right after the numbers. I conclude that the context of stimulus presentation is important in the construction of our time perception.

Chapter 4

Effect of Mode of Motor Control on Subjective Time

4.1. Introduction

Sensorimotor contingency is one of the factors that potentially affect time perception. It has been suggested that the intentional state is one of the important factors affecting the sense of time (Haggard *et al*., 2002b). The perceived timing of key pressing and the subsequent tone were shifted so that they were closer to each other, when the subject voluntarily pressed the key followed by a tone with some delay. This "temporal attraction" has been termed "intentional binding effect" (Ebert & Wegner, 2010; Engbert & Wohlschläger, 2007; Humphreys & Buehner, 2010; Moore & Haggard, 2008; Stetson *et al*., 2006; Tsakiris & Haggard, 2003). In contrast, when the movement was induced by transcranial magnetic stimulation (TMS), the temporal shift occurred in the opposite direction.

The mode of initiation of an action (intrinsic or extrinsic, i.e., self-initiated (intention-based) or externally-triggered (stimulus-based), Jahanshahi *et al*. 1995; Waszak *et al*. 2005)) is one of the important contextual factors in sensorimotor contingency. In an externally-triggered condition, a subject generates a movement as a response to a sensory stimulus. A self-initiated action, in contrast, is driven internally.

It has been suggested that different mechanisms are engaged in the intrinsic and extrinsic movements (Obhi & Haggard, 2004). Welchman *et al*. (2010) showed that the speed of action in a reactive movement was faster than in a self-timed action. Imaging studies have shown that different neural mechanisms are engaged in these movements (Herwig *et al*., 2007; Jenkins *et al*., 2000; Keller *et al*., 2006; Taniwaki *et al*., 2006). Activities in the basal ganglia (Cunnington *et al*., 2002) and

dorsolateral prefrontal cortex (François-Brosseau *et al*., 2009; Jahanshahi *et al*., 1995; Wiese *et al*., 2004) increase in self-initiated movements compared to the externally-triggered movements. In a monkey study, the firing rate of neurons in the putamen increased faster in a self-initiated than in an externally-timed movement (Lee & Assad, 2003). A study on human subjects also showed that movement-related cortical potentials in a self-initiated movement were larger than in an externally-triggered movement (Jahanshahi *et al*., 1995). The onset of hemodynamic response of pre-SMA in a self-initiated movement was earlier than in an externally-triggered movement (Cunnington *et al*., 2002).

Some studies have suggested that externally and internally initiated movements have different effects on time perception. Haggard *et al*. (2002a), for example, reported temporal attraction effects between action and auditory tone both in self-initiated and externally-triggered conditions. In a self-initiated condition, a subject intentionally pressed a key at his or her own timing, causing a tone after 200 ms. In an externally-triggered condition, on the other hand, the subject pressed the key as quickly as possible upon hearing tone. The temporal order of action and tone was reversed between the two conditions. The subject reported the perceived timings of key pressing and tone. The perceived timings of action and tone became closer to each other in both conditions, indicating that the directions of the shift of the perceived timing of tone and action were reversed between the two conditions.

Studies on chronostasis have shown that actions and subjective durations are closely linked (Yarrow *et al*., 2001: Yarrow *et al*., 2004a; Yarrow *et al*., 2004b). In this illusion, the visual stimulus presented immediately after the saccade was perceptually dilated (Yarrow *et al*., 2001). The magnitudes of the lengthening effect were similar between the controlled and automatic eye movements (Yarrow *et al*., 2004b), with a constant effect across various intervals, indicating that chronostasis was not affected by the magnitude of volition.

Park *et al*. (2003) found that not only saccades but also voluntary movements such as key press and utterance caused an overestimation of the perceived duration of its sensory feedback, extending the chronostatsis studies in context. In general, there appear to be interconnections between voluntary actions and subjective durations, a point that needs to be investigated further.

Different neural mechanisms and range of intervals are involved for saccades, finger movements, and other kinds of voluntary actions (Kandel *et al*., 2000). Thus, the results obtained in the chronostatis studies do not necessarily apply to voluntary movements in general. Identifying a common mechanism for saccades and other voluntary movements will contribute to the understanding of the relation between subjective duration and voluntary movements in the general context.

The effect of chronostasis was not affected by the context of saccade initiation (Yarrow *et al*., 2004b), and was constant across intervals (Yarrow *et al*., 2004a). It is still unknown whether such is the case for other kinds of voluntary movements (e.g. key pressing). It has been shown that the perceived timings of action and effect were affected by the sensorimotor context (Haggard *et al*., 2002a). It is possible that the subjective duration in voluntary movements such as key pressing is affected by the sensorimotor context, in contrast to chronostasis. It is interesting to investigate whether the context of action initiation would affect the estimated interval.

Here I use a temporal reproduction paradigm to investigate the effect of sensorimotor context on the perception of duration. The subjects were presented with sensory stimuli of various intervals. They were instructed to estimate the intervals and reproduce them through key pressing. In order to investigate the effect of sensorimotor contexts (e.g. self-timed versus externally-timed), the timings of the key pressing were constrained in various ways.

A voluntary movement can be classified either as an automatic or a controlled process (Wegner, 2002). An automatic movement is reflex-like and fast (~500 ms), with its conscious perception occurring after the motor execution (Welchman *et al*., 2010). On the contrary, a controlled movement requires cognitive processes depending on attention and working memory, takes longer time (>500 ms), and is more flexible. An action initiation within 500 ms after the Go signal can be regarded as an automatically controlled movement, while an action initiated between 1 and 2 s after Go signal can be regarded as cognitively controlled movement, requiring the subject to inhibit motor output for some interval while carrying it out before the deadline. Such a movement could not be achieved without a top down control. Our experimental setup incorporated these temporal constraints.

It has been suggested that different neural mechanisms are involved in the estimation of temporal duration below and above 2 - 3 s (Poppel, 1997; Ulbrich *et al*., 2007). Temporal processing of up to 2

- 3 s can be regarded as “time perception”, while those lasting more than 3 s is thought to be “time estimation” (Fraisse, 1984). In order to investigate the relation between the estimated intervals and sensorimotor contingencies, intervals in the range of 1 - 5 s were presented in the experiments, covering the “time perception” as well as the “time estimation” domains.

4.2. Methods

4.2.1 General Descriptions

I conducted three experiments. All subjects were naïve about the purpose of the present study, except that in experiments 1 and 2 subject TH was the author of this thesis. All subjects had normal or corrected-to-normal vision, and were right-handed by self-report, except for one subject in experiment 3. The experiments were conducted in accordance with the Declaration of Helsinki. The experimental procedures were submitted to and approved by the brain and cognitive sciences ethics committee of Sony Computer Science Laboratories. Informed consent was obtained from all participants.

The experiments were conducted using the self-timed and externally-timed conditions. In the self-timed condition, the subject was instructed to start the reproduction at his or her own timing. In the externally-timed condition, the subject was required to start the reproduction within a predetermined interval. There were two subconditions for the externally-timed condition. In the automatic condition, the subject was instructed to press the key within 500 ms after the trigger signal. In the controlled condition, the subject was instructed to press the key within 1 - 2 s after the trigger signal. It was assumed that the automatic and controlled conditions would induce reflex-like (Welchman *et al*. 2010) and cognitively controlled movements, respectively, the latter involving an active suppression and higher volitional states.

In Experiment 1 and experiment 2 (visual condition), the sessions were controlled by a desktop PC (EPSON Endeavor MT8800) and a 21-inch CRT monitor (Sony Trinitron CPD-G520). The subjects responded by pressing a key (SANWA SUPPLY NT-11UBK, with a keystroke of 2.2 ± 0.1mm). In

experiment 2 (auditory condition) and experiment 3, the sessions were conducted on Mac Book Pro 15 inch model. The tones were presented through a headphone (Sony MDR-XD100).

4.2.2 Experiment 1

In experiment 1, I examined the effect of movement under self-timed and externally-timed (automatic or controlled) conditions on the perception of temporal duration. In experiment 1(a), ten subjects (seven males and three females, mean age = 29.4, sd = 2.5) participated in a combination of self-timed and automatic conditions. In experiment 1(b), eight subjects (five males and three females, mean age = 29.3, sd = 2.4) participated in a combination of self-timed and controlled conditions. The subjects of experiment 1(b) were a subset of the subjects of experiment 1(a).

Before the experiment, the subjects practiced pressing the key according to the conditions. In experiment 1(a), the subjects practiced to press the key within 500 ms after the Go signal (automatic condition). The words “too late” were displayed on the screen at the passage of 500 ms after the Go signal. Typically, a practice of several times was sufficient. In experiment 1(b), the subject practiced to press the key between 1 and 2 s after the Go signal (controlled condition). After the key pressing, the subjects were given textual feedback; “too early” if the subject pressed the key before 1s after the Go signal, “SUCCESS” if the subject pressed the key between 1 and 2 s after the Go signal, and “too late” if the subject pressed the key later than 2 s after the Go signal. When a subject successfully pressed the key for ten continuous trials, the practice session was over and the experiment started. All subjects could pass this criterion within trials of up to 30.

At the beginning of each trial, a white circle (0.95°) appeared at the center of the screen, which remained until the end of each trial. The subject was instructed to keep a natural posture without crossing the legs and putting the elbow on the desk, and to fixate on the circle while keeping posture and attention. One second after the appearance of the circle, the reference auditory stimulus was presented to both ears through a headphone (Figure 4.1). The subject was instructed to memorize its duration. The duration of the reference stimulus was either 1, 3 or 5 s, presented in random order. After the offset of the reference duration, the Go signal was presented. The intervals between the

offset of the reference duration and the Go signal were randomly chosen from 1, 1.5 and 2 s, to prevent the subject from anticipating the timing of the Go signal. After the Go signal, the subject was instructed to press the designated key with their index finger of the right hand and keep pressing for a duration matching that of the reference tone. There was not an auditory feedback accompanying the key pressing. The subjects were instructed to refrain from silently counting or keeping a rhythm while they estimated the duration.

The self-timed and externally-timed (automatic or controlled) conditions were assigned to respective blocks. Before the session started, the subjects were instructed which of the self-timed, or externally timed (automatic or controlled) conditions applied to each block. The subjects conducted two blocks for each condition. The order of the conditions was counterbalanced among the subjects. The subjects were allowed to take rest between the blocks. One block consisted of six presentations of the reference duration. Thus, the reproduction of duration was conducted twelve times for each interval in respective conditions, resulting in 72 trials overall.

In the externally-timed conditions (automatic or controlled), when the subjects failed to press the key within the predetermined limits, an error feedback was presented, with the trial terminated to proceed to the next trial. The missed trials were stacked at the end of the block to be executed later. This manipulation was designed to prevent the subjects from adapting to the reference interval.

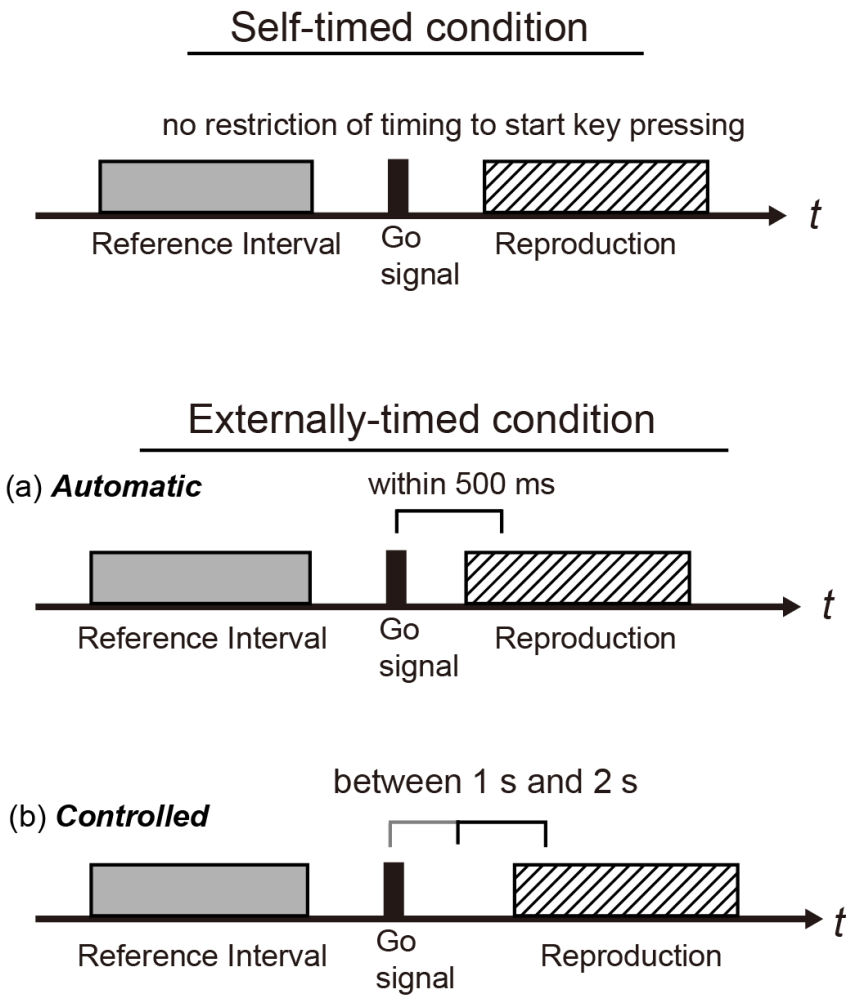


Figure 4.1 Experimental procedures in experiment 1. The subjects were instructed to memorize the reference durations presented with an auditory tone. The subjects then reproduced the intervals by keeping the key press after the Go signal. In the self-timed condition, they started reproduction by their own timing. In the externally-timed condition, the timing of pressing the key was limited to within 500 ms (**a.** automatic condition) and to between 1 s and 2 s (**b.** controlled condition) after the Go signal.

4.2.3 Experiment 2

In experiment 2, I further investigated how the difference of action initiation would affect temporal processing. In exp. 1, the movement conditions were separated by blocks, where the subjects knew which action would be required at the moment the reference intervals were presented. If the

subject's internal states such as attention and concentration varied between the movement conditions, these changes in internal states throughout the block could affect the temporal processing at the encoding period (Figure 4.2). Therefore, there was the possibility that the differences in reproduced intervals were due to those in the encoding period, not in the reproduction period. In exp. 2, the subjects reproduced the reference intervals under externally-timed (automatic or controlled) conditions, without receiving a prior instruction of which action to take before the reference intervals were presented.

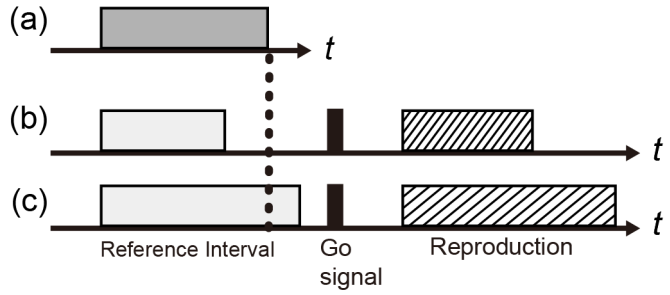


Figure 4.2 An example that a difference of reproduced intervals arises from a difference of memory of reference interval at encoding phase. (a) An actual length of reference interval. (b) A subject memorized the reference interval shorter than the actual interval. (c) The subject memorized the reference interval longer than the actual interval. The difference of memorized intervals between (a) and (b) will lead the difference of reproduced intervals. (As a matter of course, it is not important whether the memorized interval was shorter or longer than the actual interval. The point is that the difference of memorized intervals for the same interval will result in the difference of reproduced intervals.)

Five subjects (three males and two females, with average age = 29.0, sd = 2.2) participated in the auditory condition. Five subjects (three males and two females, with average age = 29.6, sd = 2.1) participated in the visual condition. The subjects were a subset of the participants in experiment 1.

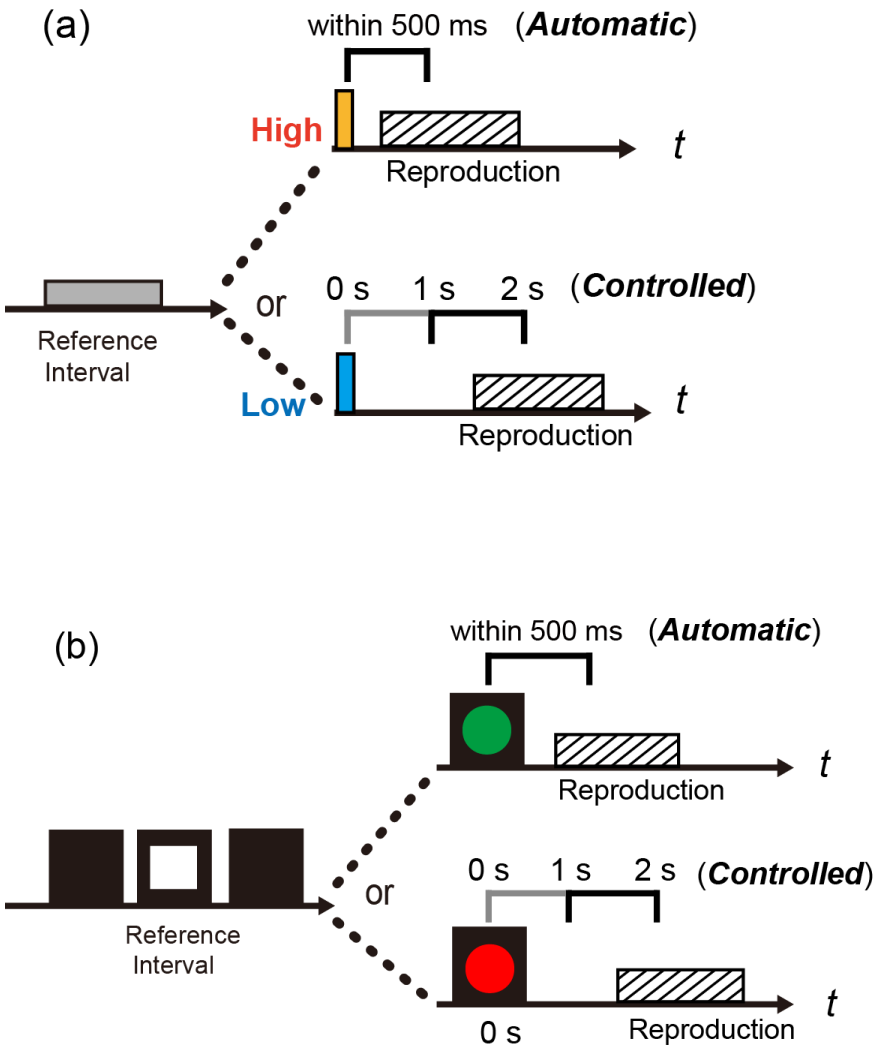


Figure 4.3 Experimental procedures in experiment 2. **a.** Auditory condition. Reference intervals were presented with the auditory tones. The subjects were instructed to remember its duration. After the Go signal, the subjects reproduced the interval of the reference by pressing the key. The Go signal was either high or low tone. The pitch of the Go signal instructed the subjects which action to conduct. In this figure, the subjects had to start the reproduction within 500 ms after the high tone Go signal (automatic condition), and between 1 and 2 s after the low tone Go signal (controlled condition). The assignment of the pitches of the Go signal to movement conditions was counterbalanced among the subjects. **b** Visual condition. The white square was presented as the reference interval. The subjects were instructed to memorize its interval. After the presentation of the square, a green or red circle appeared as the Go signal. The subjects reproduced the reference interval after the Go signal. The color of circle

instructed the subject which action to conduct. In this figure, the subjects began reproducing within 500 ms after the Go signal when the color was green (automatic condition). On the other hand, when the red circle appeared, the subjects began reproducing between 1 and 2 s after the Go signal (controlled condition). The assignment of the circle colors to movement conditions was counterbalanced among the subjects.

In the auditory condition (Figure 4.3a), a white square (1.72°) was presented for 1 s to indicate the beginning of the trial. One second after the disappearance of the square, a sound (1000 Hz, 60 dB) indicating the reference intervals was presented to the subject from the headphone. The subjects were instructed to memorize its interval. The duration of the reference intervals were 1, 3, and 5 s, presented in a random sequence. 1.5 s after the offset of the reference interval, the Go signal was presented. The Go signals were low (500 Hz) or high (2000 Hz) sound with a duration of 20 ms, one of which instructed the subject to reproduce within 500 ms after the Go signal (automatic condition), while the other instructed to start the reproduction between 1 s and 2 s after the Go signal (controlled condition). The assignments of the Go signal pitches for alternative actions were counterbalanced among the subjects.

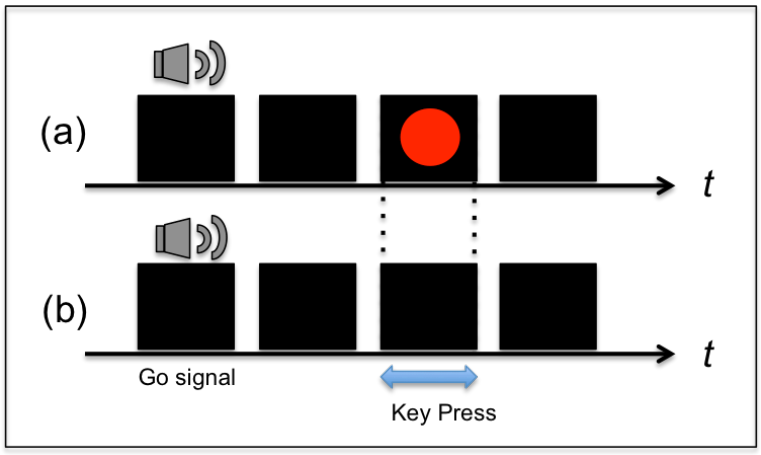


Figure 4.4 Procedure of practice session in the auditory condition. (a) In the first four trials of all (thirty four) trials, a red circle were appearing while a subject would have to press a key after Go signal. The subject learned temporal limit that she or he should press the key. (b) In the remaining trials, the subject had to press the key within the interval the red circled had been presented (the red circle was no longer presented). In the actual practice session, Go signal was high or low tone and the intervals when the red circle were presented were either within 500 ms or 1 to 2 s after Go signal. A pair between the pitch of Go signal and the temporal limit of key pressing was fixed.

Before the experiment, the subjects learned the assignment of the Go signal pitches for alternative actions. This learning session consisted of thirty-four trials in a block. In the first four trials a red circle (1.53°) was presented at the center of the screen after the Go signal (Figure 4.4). It was presented for the predetermined interval within which the subjects had to press the key in the automatic or controlled condition (appearing twice each in an interleaved manner). The subjects attended to the stimulus and learned the timing of key pressing. In the remaining thirty trials, the subjects had to press the key as indicated by the red circle on the screen in the first four trials (the automatic and controlled conditions appearing fifteen times each in a random manner). The practice session was over when the subjects successfully pressed the key within the designated time frame for more than ten cumulative times for both conditions. In the case of failure, the subjects were required to conduct one more block. Text feedbacks were provided on the timing of subjects' key pressing ("too fast", "SUCCESS", or "too late"). All the subjects cleared this criterion in less than two blocks.

The experiment started after twelve warm up trials. One block of experiment consisted of eighteen trials, in which each reference interval for respective conditions was presented three times. The subjects conducted six blocks. In all, the subjects reproduced each interval 18 times in both conditions. After the Go signal, the subjects pressed the space key on the keyboard, pressing for the duration of the remembered interval and then releasing the key. No feedback was presented to the subjects during the key pressing. The next trial started 1.5 s after the subject keyed off. The subjects were instructed not to use the strategy of counting or keeping rhythm during the encoding and reproduction of the interval.

In the visual condition, a white square (3.34°) was presented as the reference for 1, 3 or 5 s (Fig. 4.3b). After the reference stimulus, a color (red or green) circle (1.91°) was presented for 50 ms as the Go signal. In the automatic condition, the subjects were instructed to press the key within 500 ms after the Go signal. In the controlled condition, the timing of key pressing was between 1 and 2 s after the Go signal. The green or red circle instructed the subjects which action to conduct. The two colors were randomly presented. The associations between the color and action were counterbalanced among the subjects.

Before the experiment, the subjects learned the association between colors and actions (automatic or controlled) in the practice session, where one of the alternative Go signals was presented randomly, and the subjects practiced to press the key within the predetermined limit after the Go signal. The subjects then practiced the experimental task, in which they learned to correctly estimate and reproduce the reference intervals. In one block, each reference interval for each condition was presented three times, resulting in a total of eighteen trials. The subjects conducted six blocks. They reproduced each interval 18 times in both conditions.

As in previous experiments, the subjects reproduced the presented interval by continuously pressing the key. There was no feedback while they were pressing the key.

4.2.4 Experiment 3

In experiment 3 (control), I investigated whether the delay between the presentation of the reference and reproduction affected the reproduced intervals. Seven subjects (three males and four females, with average age = 31.4, sd = 3.4) participated. Six out of the seven were the subjects in experiment 1.

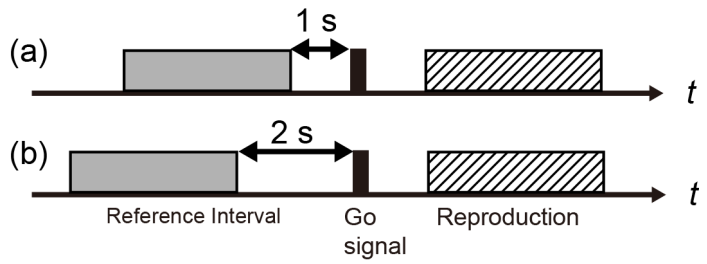


Figure 4.5 Experimental procedure in experiment 3. The interval between the offset of reference interval and the onset of Go signal was set to (a) 1 s and (b) 2 s.

In the experiment, a fixation appeared for 1 s at the center of the monitor, followed by a blank screen of 1 s. A sine wave sound (1000 Hz, 60 dB) was presented through the headphone as the reference interval. Reference intervals of 1, 3 or 5 s duration were presented in random order. The subjects were instructed to memorize the durations of the reference sound. After the presentation of the reference interval, the Go signal (sine wave, 2000 Hz) was presented. The interval (fixed throughout the block) between the offset of reference and the Go signal was 1 or 2 s. The two intervals were switched alternatingly with the conditions. The order of the two conditions was counterbalanced among the subjects.

The subjects were instructed to press the key to reproduce the reference interval at their own timing after the Go signal. One block consisted of 18 trials, in which each reference interval was presented six times. There were 74 trials in total, in which the subjects reproduced each reference interval 12 times for each condition. Before the experiment, the subjects conducted 10 practice sessions, in which the interval between the offset of reference interval and the Go signal was 1.5 s.

4.3 Results

4.3.1 General Descriptions

The measures used for investigating the effect of movement condition on temporal processing were the mean reproduction intervals, the ratio between reproduced and reference intervals, and the coefficient of variation (CV, standard deviation divided by the mean). The mean produced interval would indicate directly how the subject perceived and reproduced each reference interval. If the movement conditions affected temporal processing critically, the mean reproduced intervals would be significantly different between the conditions. The ratio between the reproduced and reference intervals would represent the degree of deviation of the reproduced interval from the actual stimuli. The CV values would indicate the variability of temporal reproduction within the subject. As noted in the discussion section, CV is one of the useful measures for investigating cognitive models of time perception.

4.3.2 Experiment 1

Table 4.1 and Figure 4.6 (a) show the results for the self-timed and automatic conditions in experiment 1. The reproduced intervals were significantly longer than the actual intervals at 1 s (one sample t-test, $t(9) = 8.75$, $p < 0.001$) and 3 s ($t(9) = 2.86$, $p = 0.018$), but were not significantly different at 5 s ($t(9) = 0.72$, $p = 0.48$) in the self-timed condition. In the automatic condition, only the reproduced interval at 1 s ($t(9) = 4.02$, $p < 0.01$) was significantly different from the actual interval (3 s: $t(9) = 1.94$, $p = 0.083$, 5 s: $t(9) = -0.19$, $p = 0.85$).

The mean reproduced intervals, ratio and CVs were submitted to a 2 × 3 repeated measures analysis of variance (ANOVA). The movement conditions (automatic versus self-timed) and the reference intervals (1, 3, 5 s) were a categorical variable and a covariate, respectively. The reproduced intervals were significantly different between the conditions ($F(1,9) = 8.17$, $p = 0.018$). The effect of reference intervals was also significant ($F(1,9) = 96.79$, $p < 0.00001$), indicating that the subjects

were sensitive to the intervals and could discriminate the durations. Their interaction was not significant ($F(1,9) = 4.86$, $p = 0.054$). For the ratio, the effect of reference interval was significant ($F(1,9) = 102.77$, $p < 0.00001$). The effect of movement condition ($F(1,9) = 4.16$, $p = 0.072$) and the interaction ($F(1,9) = 0.089$, $p = 0.77$) were not significant. For CVs, ANOVA detected a significant effect of reference interval ($F(1,9) = 9.01$, $p = 0.014$) but not for the movement condition ($F(1,9) = 1.47$, $p = 0.25$) and their interaction ($F(1,9) < 0.0001$, $p = 0.99$), indicating that the subjects attended equally to the two movement conditions.

The timings of key pressing for reproduction initiation after the Go signal were 319 ± 25ms and 1272 ± 391 ms (mean ± sd) in the automatic and the self-timed conditions, respectively, with a significant difference between them (paired t-test, $t(9) = 7.43$, $p < 0.0001$). The timing of the key pressing in the automatic condition was significantly smaller than the designated limit of 500 ms (paired t-test, one tail, $t(9) = -23.86$, $p < 0.000001$), confirming that 500 ms was a sufficient interval to press the key in response to the Go signal.

Table 4.2 and Figure 4.5 (b) show the mean reproduced intervals, ratio and CVs for each reference interval for the self-timed and controlled conditions in experiment 1. The reproduced intervals were significantly longer than the actual interval at 1 s (one sample t-test, $t(7) = 8.49$, $p < 0.001$) and 3 s ($t(7) = 4.13$, $p < 0.01$), but not at 5 s ($t(7) = -0.39$, $p = 0.70$) in the self-timed condition. Similarly, in the controlled condition, the reproduced intervals at 1 s ($t(7) = 11.82$, $p < 0.001$) and 3 s ($t(7) = 3.04$, $p = 0.018$) were significantly longer than the actual duration, but not so at 5 s ($t(7) = 0.20$, $p = 0.84$).

As in the automatic condition, the data were submitted to the 2 × 3 repeated measures ANOVA. The reference interval significantly affected the reproduced intervals ($F(1,7) = 89.85$, $p < 0.0001$). In contrast to the automatic condition, the effect of the movement condition on reproduced interval was not significant ($F(1,7) = 0.49$, $p = 0.50$). The interaction between the movement condition and the reference interval was also not significant ($F(1,7) = 1.04$, $p = 0.34$). In the case of the ratio, the effect of reference interval was significant ($F(1,7) = 111.05$, $p < 0.0001$). Neither the effect of movement condition ($F(1,7) = 0.30$, $p < 0.60$) nor the interaction ($F(1,7) = 0.001$, $p = 0.98$) was significant.

The ANOVA showed that the CVs were significantly different between different reference intervals ($F(1,7) = 5.70$, $p = 0.048$). The effect of the movement condition ($F(1,7) = 4.56$, $p = 0.069$)

and the interaction between the reference interval and the movement condition was not significant ($F(1,7) = 0.74$, $p = 0.41$).

Contrary to the automatic condition, the subjects started the temporal reproduction earlier after the Go signal in the self-timed condition (mean ± sd, 1266 ± 249 ms) than in the controlled condition (1530 ± 97 ms). The timing of starting reproduction was significant (paired t-test, $t(7) = -0.59$, $p = 0.035$), suggesting that the difference of reproduced intervals in experiment 1(a) was not simply the result of the delay between the Go signal and the timing of key pressing. If the latency of key pressing had a significant effect on reproduced intervals, there would have been significant differences of reproduced intervals here.

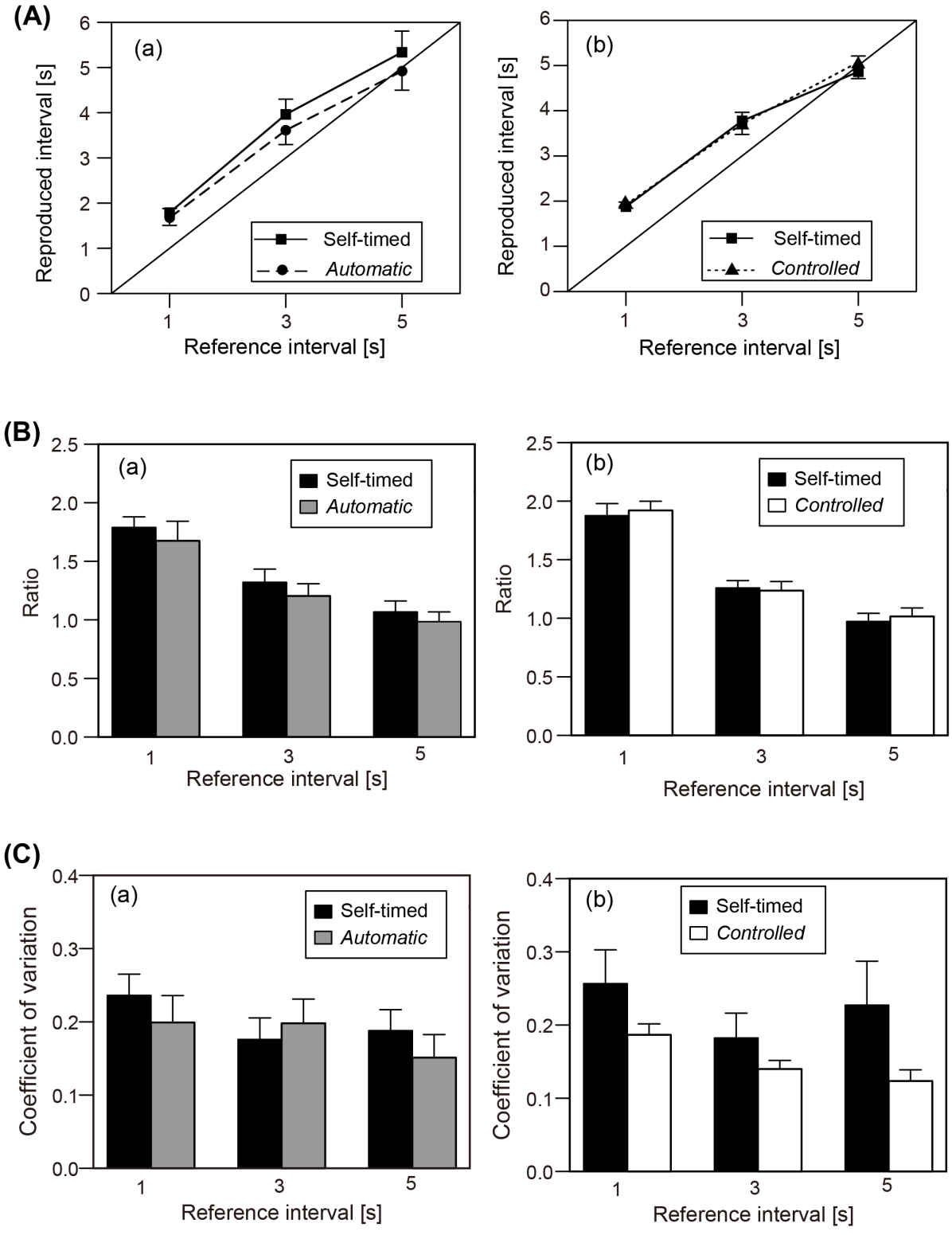


Figure 4.6 Results of experiment 1. **(A)** Mean reproduced intervals. **(B)** Ratios between the reproduced interval and the reference interval. **(C)** The coefficients of variation in Experiment 1 **(a)** and **(b)**. A skew line in the figure of reproduced interval represents the accurate reproduction. Error bars indicate SEM.

Table 4.1 Mean reproduced interval, ratio between the reproduced interval and the reference interval in Exp. 1 (a). The numbers in parentheses are standard deviation.

Movement condition	Self-timed			Externally-timed (*Automatic*)		
Reference interval	Mean	Ratio	CV	Mean	Ratio	CV
1	1.79 (0.27)	1.79 (0.27)	0.24 (0.09)	1.67 (0.50)	1.67 (0.50)	0.20 (0.11)
3	3.96 (1.01)	1.32 (0.34)	0.18 (0.09)	3.61 (0.94)	1.20 (0.31)	0.20 (0.10)
5	5.34 (1.40)	1.07 (0.28)	0.19 (0.09)	4.92 (1.26)	0.98 (0.25)	0.15 (0.09)

Table 4.2 Mean reproduced interval, ratio between the reproduced interval and the reference interval in Exp. 1 (b). The numbers in parentheses are standard deviation.

Movement condition	Self-timed			Externally-timed *(Controlled*)		
Reference interval	Mean	Ratio	CV	Mean	Ratio	CV
1	1.88 (0.27)	1.88 (0.27)	0.26 (0.12)	1.92 (0.21)	1.92 (0.21)	0.19 (0.04)
3	3.78 (0.50)	1.26 (0.17)	0.18 (0.09)	3.71 (0.62)	1.24 (0.21)	0.14 (0.03)
5	4.86 (0.92)	0.97 (0.18)	0.23 (0.16)	5.08 (0.96)	1.02 (0.19)	0.12 (0.04)

4.3.3 Experiment 2

Results for the mean reproduced interval, ratio and CV in the auditory condition of experiment 2 are shown in Table 4.3 and Figure 4.7 (a). The reproduced intervals were significantly longer than the actual interval at 1 s in both the automatic and controlled conditions, and at 3 s in controlled condition. (one sample t-test, automatic condition: 1 s ($t(4) = 4.93$, $p = 0.0078$), 3 s ($t(4) = 2.32$, $p = 0.080$), 5 s ($t(4) = 0.17$, $p = 0.86$) , controlled condition: 1 s ($t(4) = 5.88$, $p = 0.0041$), 3 s ($t(4) = 2.95$, $p = 0.041$), 5 s ($t(4) = 0.72$, $p = 0.50$).

A 2 × 3 repeated measures ANOVA detected significant effects of movement conditions ($F(1,4) = 35.84$, $p = 0.0039$) and reference interval ($F(1,4) = 37.54$, $p = 0.0035$). The effect of the interaction was not significant ($F(1,4) = 0.053$, $p = 0.82$). As for the ratio, both the effect of movement condition

($F(1,4) = 14.39$, $p = 0.019$) and reference interval ($F(1,4) = 49.29$, $p = 0.0022$) were significant, while the interaction of them was not significant ($F(1,4) = 4.92$, $p = 0.091$).

I submitted the CVs to a 2 × 3 repeated measures ANOVA. The effects of the reference interval ($F(1,4) = 7.85$, $p = 0.048$) was significant. The effect of the movement conditions ($F(1,4) = 1.43$, $p = 0.29$) and the interaction ($F(1,4) = 1.12$, $p = 0.34$) were not significant.

The latency from the Go signal to the key pressing was 357 ± 34 ms (mean ± sd) and 1409 ± 143 ms in the automatic and controlled conditions, respectively. The latency was confirmed to be different between conditions (paired t-test, one-tailed, $t(4) = -15.10$, $p < 0.0001$).

Results for the reproduced interval, ratio and CV in the visual condition of experiment 2 are shown in Table 4.4 and Figure 4.7 (b). The reproduced intervals were significantly longer than the actual intervals at 1 s, but not at 3 s and 5 s in both the automatic and controlled conditions (one sample t-test, automatic condition: 1 s ($t(4) = 4.06$, $p = 0.015$), 3 s ($t(4) = 0.55$, $p = 0.61$), 5 s ($t(4) = -1.11$, $p = 0.32$), controlled condition: 1 s ($t(4) = 4.20$, $p = 0.013$), 3 s ($t(4) = 1.45$, $p = 0.22$), 5 s ($t(4) = -0.34$, $p = 0.75$).

A 2 × 3 repeated measures ANOVA detected significant effects of movement conditions ($F(1,4) = 8.90$, $p = 0.040$) and reference interval ($F(1,4) = 14.94$, $p = 0.018$) but not their interaction ($F(1,4) = 0.28$, $p = 0.62$). For the ratio, the significant effects of the movement condition ($F(1,4) = 10.56$, $p = 0.031$), the reference interval ($F(1,4) = 17.32$, $p = 0.014$) and their interaction ($F(1,4) = 13.56$, $p = 0.021$) were detected.

I submitted the CVs to a 2 × 3 repeated measures ANOVA. The effect of the reference interval ($F(1,4) = 3.38$, $p = 0.13$), movement conditions ($F(1,4) = 0.55$, $p = 0.49$) and the interaction of them ($F(1,4) = 0.028$, $p = 0.87$) were not significant.

The latencies from the Go signal to the key pressing were 380 ± 10 ms (mean ± sd) and 1350 ± 130 ms in the automatic and controlled conditions, respectively. The latency was different between the automatic and controlled conditions (paired t-test, one-tailed, $t(4) = -15.97$, $p < 0.0001$).

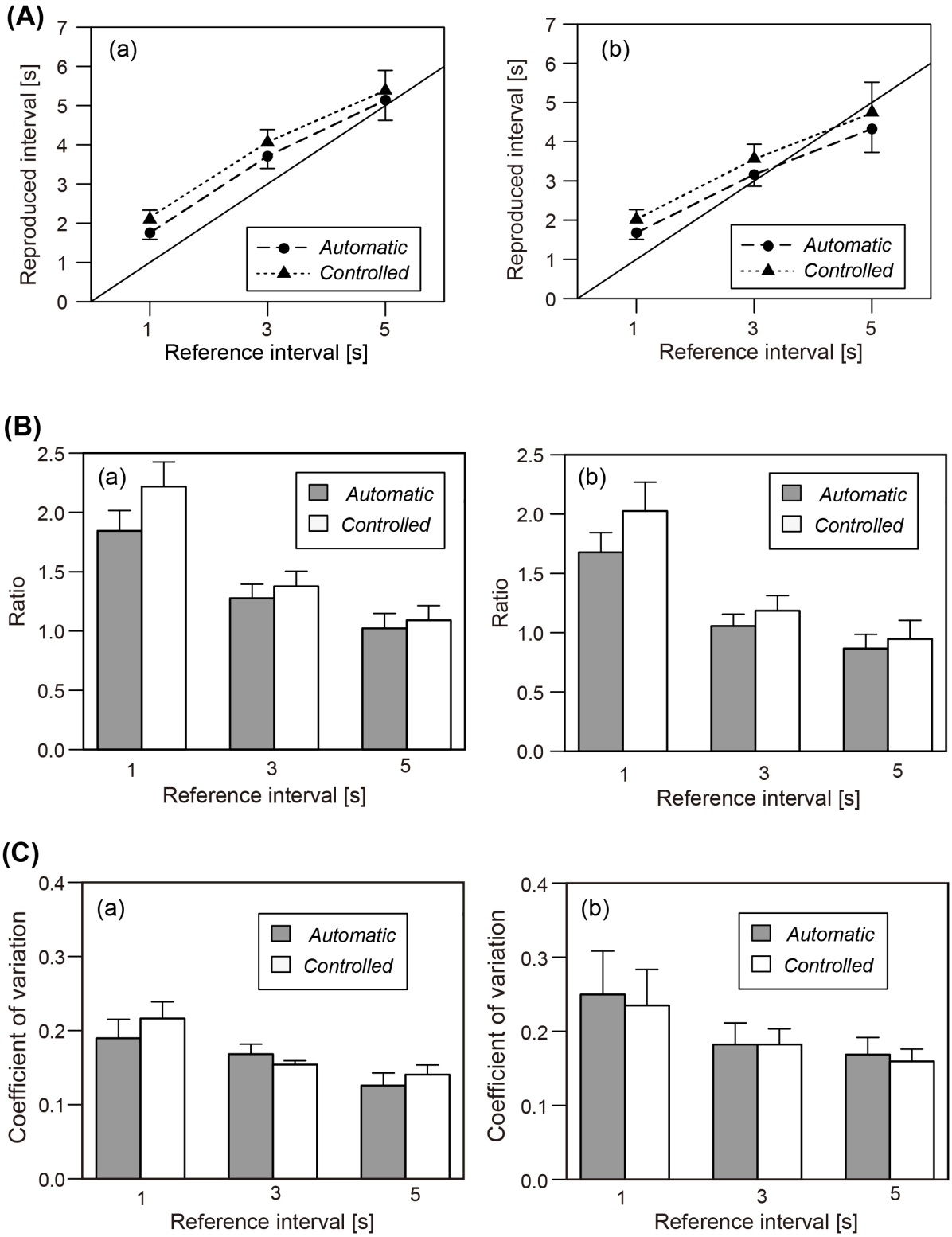


Figure 4.7 Results of experiment 2. **(A)** Mean reproduced intervals. **(B)** Ratios between the reproduced interval and the reference interval. **(C)** The coefficients of variation in the (**a)** auditory and (**b)** visual conditions. A skew line in the figure of reproduced interval represents the accurate reproduction. Error bars indicate SEM.

Table 4.3 Mean reproduced interval, ratio between the reproduced interval and the reference interval of Auditory condition in Exp. 2. The numbers in parentheses are standard deviation.

Movement condition	Automatic			Controlled		
Reference interval	Mean	Ratio	CV	Mean	Ratio	CV
1	1.84 (0.34)	1.84 (0.34)	0.18 (0.06)	2.22 (0.41)	2.22 (0.41)	0.21 (0.05)
3	3.83 (0.71)	1.28 (0.24)	0.16 (0.02)	4.13 (0.76)	1.38 (0.25)	0.15 (0.01)
5	5.11 (1.26)	1.02 (0.25)	0.12 (0.04)	5.45 (1.24)	1.09 (0.25)	0.13 (0.02)

Table 4.4 Mean reproduced interval, ratio between the reproduced interval and the reference interval of Visual condition in Exp. 2. The numbers in parentheses are standard deviation.

Movement condition	Automatic			Controlled		
Reference interval	Mean	Ratio	CV	Mean	Ratio	CV
1	1.68 (0.33)	1.68 (0.33)	0.25 (0.12)	2.03 (0.49)	2.03 (0.49)	0.23 (0.10)
3	3.17 (0.60)	1.06 (0.20)	0.18 (0.06)	3.55 (0.77)	1.18 (0.26)	0.18 (0.04)
5	4.33 (1.20)	0.87 (0.24)	0.17 (0.05)	4.73 (1.57)	0.95 (0.31)	0.16 (0.03)

4.3.4 Experiment 3

Table 4.5 and Figure 4.8 show the mean reproduced intervals, ratio and CVs in experiment 3. When reproduced intervals were submitted to a 2 × 3 repeated measures ANOVA, a significant effect of reference interval ($F(1, 6) = 135.89$, $p < 0.0001$) was detected. Neither the effect of movement condition ($F(1,6) = 1.28$, $p = 0.30$) nor the interaction ($F(1,6) = 0.52$, $p = 0.49$) was significant. For the ratio, the effect of reference interval was significant ($F(1,6) = 12.99$, $p = 0.011$). The effect of movement condition ($F(1,6) = 2.26$, $p = 0.18$) and interaction ($F(1,6) = 1.93$, $p = 0.21$) were not significant.

I submitted the CVs to a 2 × 3 repeated measures ANOVA. The effect of the reference interval ($F(1,6) = 2.79$, $p = 0.14$), movement conditions ($F(1,6) = 0.093$, $p = 0.77$) and the interaction ($F(1,6) = 2.16$, $p = 0.19$) were not significant.

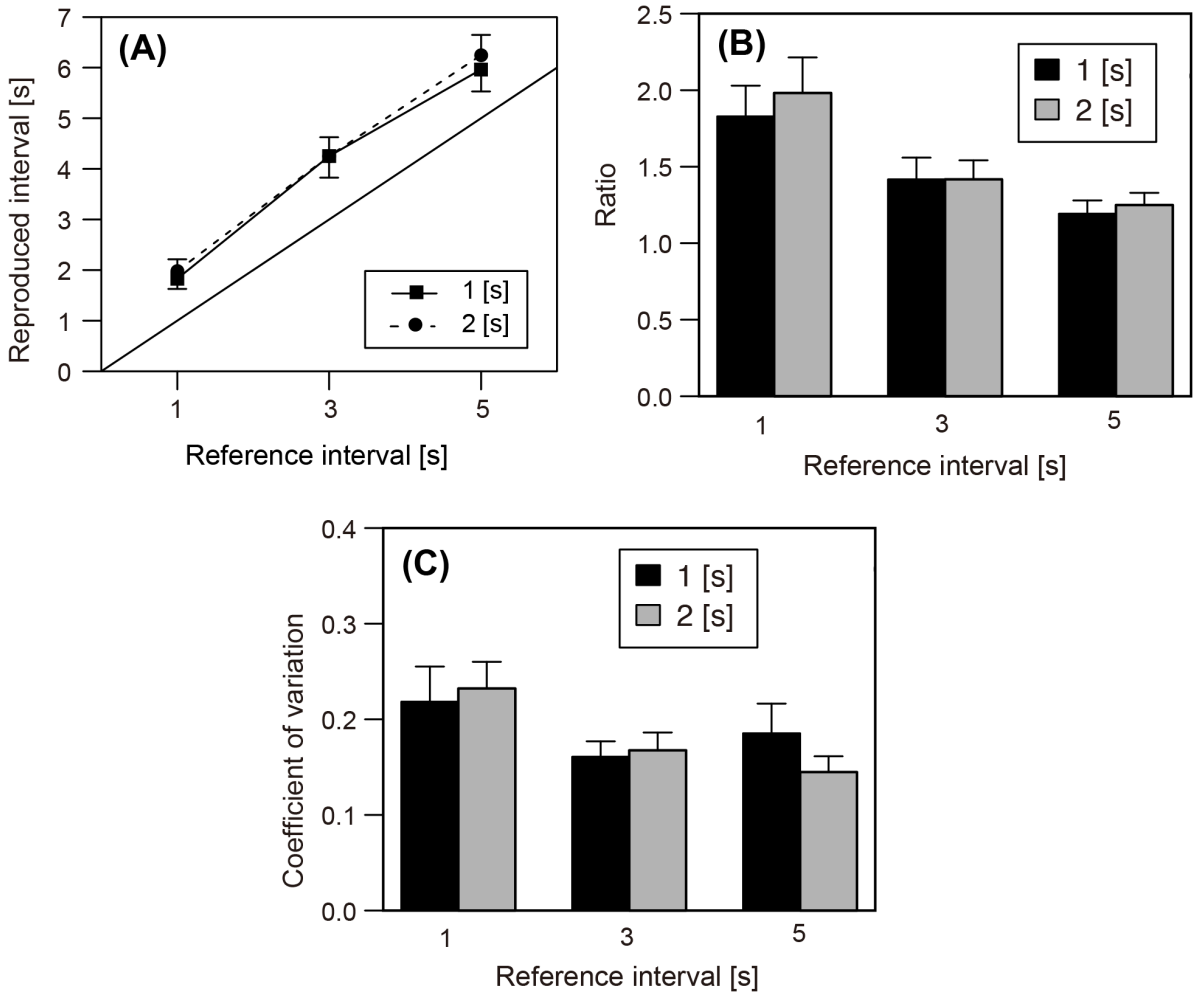


Figure 4.8 Results of experiment 3. **(A)** Mean reproduced intervals. **(B)** Ratios between the reproduced interval and the reference interval. **(C)** Coefficients of variation. The number of seconds in the legend indicates the interval between the reference interval and the Go signal. A skew line in the figure of reproduced interval represents the accurate reproduction. Error bars indicate SEM.

Table 4.5 Mean reproduced interval, ratio between the reproduced interval and the reference interval in Exp. 3. The numbers in parentheses are standard deviation.

Delay [a]	1s			2s		
Reference interval	Mean	Ratio	CV	Mean	Ratio	CV
1	1.83 (0.49)	1.83 (0.49)	0.22 (0.09)	1.98 (0.57)	1.98 (0.57)	0.23 (0.07)
3	4.25 (1.04)	1.42 (0.35)	0.16 (0.04)	4.25 (0.91)	1.42 (0.30)	0.17 (0.05)
5	5.96 (1.06)	1.19 (0.21)	0.19 (0.08)	6.25 (0.98)	1.25 (0.20)	0.14 (0.04)

a. Deley indicates the interval between the offset of reference and the Go signal.

4.4 Discussion

In this study, the subjects reproduced the reference intervals by pressing the key. The purpose of this study was to investigate whether the subjective duration was affected by the nature of voluntary movement of key pressing in various contexts of action initiation. In addition, I examined how the effect on temporal reproduction varied as a function of the reference intervals.

The results for experiment 1 suggest that when the subject pressed the key in a reflex-like manner (within 500 ms, automatic condition), the reproduced intervals became shorter compared to the timing of self-timed key pressing. Limiting the timing of key press between 1 and 2 s after the Go signal (controlled condition) presumably made the action highly volitional and cognitively controlled, as the subject was required to suppress the movement for some time and then initiate the movement before the deadline. This suppression would have necessitated cognitive modulations from top-down control circuits including the prefrontal brain area. These results suggest that the temporal estimation was not significantly different between self-timed and cognitively controlled movements. On the other hand, the reproduced interval in self-timed condition was significantly different from the automatic condition, suggesting that the automaticity of action initiation has a significant effect on interval estimation within the range of several seconds.

The results of experiment 2 suggest that when the subjects started the reproduction in the automatic and reflex-like manner, their reproduced intervals were significantly shorter than when movements were initiated in a cognitively controlled manner. Since the subjects did not know which movement condition would occur when the reference intervals were encoded, the difference of reproduced interval could not be attributed to the encoding phase. Comparison with results of experiment 1 would suggest that the online estimation of interval was affected by the context of action initiation. The results of auditory and visual conditions also suggest that the effect was independent of the modalities. These results are consistent with a model involving a common timing mechanism for both visual and auditory modalities.

The results of experiment 3 show that the delay of reproduction period did not affect the reproduced interval. It has been suggested that the interval between encoding and reproduction period affected the reproduced interval (Wearden *et al*., 2007). The delay used in Wearden *et al*. (2007), however, was longer than those employed in our present experiments. In addition, they showed that longer delays shortened memorized intervals, contrary to our results in experiments 1 and 2. Therefore, the interval between the offset of the reference interval and the timing of key press might not be a critical factor for the reproduced interval in our experiment. The differences of reproduced intervals are likely to have been caused by the contexts in which the movements were initiated.

It has been suggested that different mechanisms are engaged in the processing of intervals under and above about 3 s (termed "time perception" and "time estimation", respectively, Fraisse, 1984; Poppel, 1997; Ulbrich *et al*. 2007). In experiments 1 and 2, the interactions between the reference interval and the movement condition were not significant. Thus, the effect of the movement condition on duration reproduction was constant over these ranges, suggesting that a common mechanism might underlie "time perception" and "time estimation".

In a review of brain imaging studies, Lewis and Miall (2003a, 2006) suggested that different brain networks were engaged in temporal processing, depending on whether the movements were automatic or cognitively controlled (Figure 4.9). Cognitively controlled timing task involves the right dorsolateral prefrontal cortex (rDLPFC) and the right posterior parietal cortex (rPPC). On the other hand, automatically controlled timing task involved the supplementary motor area (SMA), left sensorimotor cortex, and the right cerebellum.

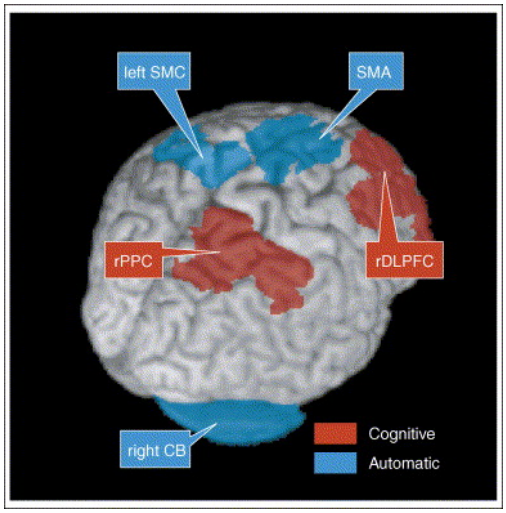


Figure 4.9 The brain regions which were engaged in cognitive controlled (red) and automatic (blue) timing task. Abbreviations: CB, cerebellum; SMA, supplementary motor area; SMC, sensorimotor cortex; rPPC, right posterior parietal cortex; rDLPFC, right dorsolateral prefrontal cortex. Adapted from Lewis and Miall (2006).

It is possible that the significant difference of reproduced intervals in different movement conditions resulted from the activation of different neural networks between the conditions, while the absence of the significant differences in reproduced durations between the self-timed condition and controlled condition in experiment 1 is due to the fact that similar networks were activated in the two conditions. For example, the dorsolateral prefrontal cortex might be activated and play a significant role in both self-timed and cognitively controlled movements.

In the present study, some results were consistent with those in the previous studies of chronostasis, while others were contradictory. As is the case with the chronostasis (Yarrow *et al*., 2004a), the effect size was constant across the estimated intervals. Our results, on the other hand, showed that when the subject began the temporal reproduction in a reflex-like manner (automatic condition), the reproduced intervals were shorter than those in the self-timed or cognitively controlled actions (controlled condition). This result is in contradiction to the results obtained in the study of chronostasis in which the lengthened effects by saccades were not significantly different between the high volitional and reflex-like eye movements (Yarrow *et al*., 2004b). Yarrow *et al*. (2004b) concluded that the effect of chronostasis was triggered by an efference signal arising in the superior colliculus. The difference

between our results and the chronostasis studies may be attributed to the difference in the neural mechanism of saccades and finger movements, and the range of estimated intervals involved.

Our results suggest relative differences of interval estimation depending on the movement conditions. The automatic action might have dilated the subjective duration, while the self-timed and cognitively controlled action might have compressed it. It is also possible that both effects have co-existed.

Some features of the present results can be explained by the SET model, which is one of the applications of internal clock model. Specifically, the results presented here show that the difference of estimated intervals between action contexts were constant across the range of estimated intervals. A change in the clock rate would predict a proportional difference as a function of the interval, while a change in the latency of closing switch would predict a constant difference regardless of the estimated intervals. Our results are compatible with an account in terms of the closing latency: When the subjects initiated action in a reflex-like manner (automatic condition), the latency of closing switch was shorter.

Our results showed that the CV values decreased as a function of estimated durations. The decrease in CV values is consistent with the results of Ulbrich *et al*. (2007), where the subjects reproduced intervals between 1 and 5 s. On the other hand, the SET model predicts that CV would be constant for changes of the interval. The discrepancies indicate that the SET model might have to be modified. It is possible that different mechanisms are engaged in measuring a temporal interval, depending on whether the interval is shorter or longer than about 3 s (Fraisse, 1984; Poppel, 1997; Ulbrich *et al*. 2007). Higher cognitive processes would be involved in the processing of longer intervals. Measurement of shorter intervals would be carried out mainly by lower neural mechanisms, where temporal processing may be affected by various noises. Because of these noises, the measured duration would be variable for shorter intervals. When the target interval is longer, the higher cognitive processes would be engaged in measuring the duration. The higher cognitive processes may compare the interval being measured with the interval stored in memory and compensate for the deviation caused by the noises. As a result, the measured intervals for longer durations would have

lower variability than for the shorter ones. Such a compensating mechanism might have to be incorporated to supplement the SET model.

There are alternative explanations for our results. Wenke and Haggard (2009) investigated how a subject's sense of time changed when a temporal attraction happened. The results indicated that the threshold for a successful temporal discrimination for tactile stimuli on the subject's finger became larger when the stimuli were presented right after their action, while the subjects pressed the key voluntarily. Within the framework of internal clock model, the clock would have slowed down transiently by the initiation of voluntary movements. Although their study suggested that this effect occurred only when the action led to a sensory feedback such as an auditory tone, our results can be explained by this transient clock rate change assumption. A slower clock rate in the self-timed condition would lead to longer reproduced intervals than in the reactive movement condition (i.e., the automatic condition). In addition, the opposite effect, in which the rate of the internal clock became faster transiently, can also be considered. Welchman *et al*. (2010) showed that reactive action was conducted quicker than self initiated movements. This phenomenon suggests that the progress of the internal clock would get transiently faster when the subjects initiated a movement in a reflex-like manner. This consideration also fits the present results, as a faster speed of internal clock would lead to shorter reproduced interval (Figure 4.10). It is possible that either one or both effects led to the present results.

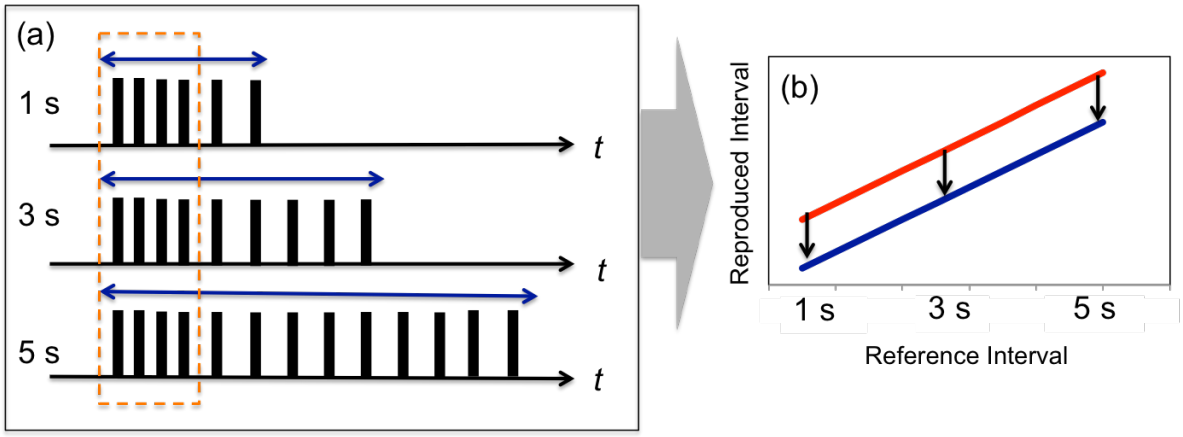


Figure 4.10 A transient acceleration of the internal clock results in a downward parallel shift of reproduced intervals. (a) The transient change of the internal clock rates at reproduction phase in the automatic movement condition. Each temporal axis represents reproduction phase for each reference interval (1, 3 and 5 s from top to bottom). A black rectangle on the axis indicates a pulse that the internal clock emits. The clock rate becomes faster transiently after key pressing and then it gets back to at normal rate. A time span (an area surrounded by a dotted line), within which the clock rate changes, is alike regardless of temporal length a subject tries to reproduce. (b) A prediction from the condition of (a) for reproduced intervals. Lines indicate reproduced interval for each reference interval. When the internal clock increases transiently regardless of reproduced intervals, a constant decrease across reproduced intervals will be observed.

In experiment 1, the automatic and controlled conditions with limits on the timing of key press were more demanding than the self-timed condition. Therefore, the subject's attentional allocation might have been different between these conditions. Task difficulty is known to affect temporal processing (Zakay *et al*., 1983). The dual task paradigm studies have also suggested that loads of temporal and nontemporal concurrent tasks affected the attentional allocation and resulted in the temporal processing of other tasks (interference effect) (Brown & West, 1990; Brown, 1997; Dutke, 2005). A concurrent task such as visual search and arithmetic demands attentional resources and interfere with the subject's temporal task, leading to a decrease in the pulses accumulated in the memory system. In view of these results, in our experiments, it is possible that pressing the key within the predetermined time limit demanded in the subjects some degree of attentional allocation, resulting in longer durations in the externally-timed conditions (automatic and controlled) than in the self-timed

condition. Subjects who participated both in the automatic and controlled conditions in experiment 1 reported that the latter was more difficult to execute than the former. If the task load and attentional allocation affected the temporal reproduction period critically, the reproduced intervals in the automatic condition would be longer than those in the self-timed condition. In addition, the dilation of reproduced intervals in the controlled condition compared to those in the self-timed condition would be more enhanced than in the case of automatic condition. However, such were not the case. Therefore, I conclude that it is not likely that attention and task load led to the present results.

In the controlled condition, before starting the reproduction of reference interval, the subjects had to estimate a duration of 1 - 2 s. There is thus a possibility that this additional temporal estimation process might have affected the following reproduction process of reference interval.

However, when comparing the CV of the controlled condition with other conditions in experiment 1 (b) and experiment 2, the statistical analysis did not detect significant differences, indicating that the variability of the reproduced intervals were not statistically different whether there was an additional temporal estimation before the reproduction. In addition, in experiment 1 (b), the reproduced intervals were not significantly different between the self-timed and controlled conditions, indicating that the additional estimation of the interval of 1 - 2 s before the reproduction of reference interval did not affect the reproduced interval significantly. Based on these observations, I conclude that the estimation of 1 - 2 s in the controlled condition did not significantly affect the reproduction process.

In sum, I investigated the effect of the context of action initiation on temporal reproduction. The subjects reproduced three kinds of reference intervals by pressing the key. When the subjects tried to reproduce the duration by reflex-like movements, the reproduced intervals were significantly shorter than those for self-timed and cognitively controlled movements. In the context of the internal clock model, these results would indicate that when the subjects initiated to move in a reflex-like manner, the latency of switch closing would be faster, or the clock speed would become faster. Such changes would affect the perception of duration, as a result of the interaction between our action and environment.

Chapter 5

General Discussion

In this thesis, I focused on subjective time and conducted two experiments to investigate effects of perceptual context (order of number) and motor context (mode of motor control) on temporal processing in Chapter 3 and 4, respectively.

The result of Chapter 3 showed that the order of digits (ascending or descending) affected perceived duration of the following stimulus. When the digits from one to nine were presented in the ascending order, the perceived duration of the following target square was longer than when the digits were presented in the descending order. The result of control experiment, in which only the last digits of the ascending or the descending order was presented before the target, implicated that this effect might not be caused by the number before the target. The significant effect of digit order was not observed when the total number of presented digits was reduced from nine to five, suggesting that continuous context to some extent was needed to induce measurable differences of temporal processing.

The result of Chapter 4 showed that the mode of motor control (e.g., automatic, cognitive-controlled, and self-timed) affected the reproduced intervals of memorized reference intervals. In this experiment, the subject memorized the reference interval and reproduced it by keeping pressing the key. The differences of mode of motor control were set in the beginning of key pressing (i.e., the start of reproduction of memorized interval). When the key press was started by automatic action, the reproduced intervals were shorter than when the key press was started by self-timed or cognitive controlled action. The experiment also showed that neither the differences of the internal state at the encoding phase nor the duration of retention caused the differences of reproduced interval.

I think that the results in Chapter 4 are also important for a field of engineering. For example, when using a tablet or a smartphone, even though an actual timing of feedback of tapping on a screen is the same, perceived timing or duration are different depending on the mode of motor control of user. It might be possible that subjective sense of time was different whether they are playing a game, chatting, or watching movies. So a designer or a programmer of an application have to analyze what kind of application they are going to make and take this property of subjective time into account in order to produce a better application. In addition, when designing a brake of a car, it is thought that understanding these properties of subjective time might be useful in order to enhance user experience. When a child rushes out suddenly in front of the car, we put on the braking automatically. On the other hand, our action to put on the braking may be controlled action when we prepare braking in advance such as on a red light. A driver's subjective sense of time will be different between these situations.

Although one of the experiments was the perceptual temporal task and the other was the motor temporal task, there was a common part between these two temporal tasks. For both experiments, the context before the subject began to estimate duration affected the perceived duration. In chapter 3, it was the order of numbers. In chapter 4, it was the mode of motor control. It indicated that our subjective time is affected by a prior context and changed dynamically.

There were studies which showed that accuracies of timings of motor and perception were related (Ivry & Hazeltine, 1995). There were correlations between performance of motor timing task and that of perceptual timing task across subjects (Keele *et al*., 1985; Merchant *et al*., 2008). It meant that the subject who showed higher temporal accuracy in motor timing task tended to show higher temporal accuracy in perceptual timing task. In addition, training of perceptual timing task enhanced an accuracy of motor timing task (Meegan *et al*., 2000). Subjects were divided into two groups and the both groups trained perceptual temporal discrimination task. A target interval that the one group trained was 300 ms and the other was 500 ms. After the training, improvements of performances of motor timing task were larger at the interval they trained than they did not. It indicated that the temporal processing of perception and motor might be processed by some common neural mechanisms.

In the future research, one of directions is to investigate what the results of experiments in this thesis suggested. In the experiment in Chanter 3, it is still unknown whether the continuous changes of magnitude other than digits (e.g., size of shape and brightness) would also affect subjective duration of a following stimulus. It may be interesting to investigate whether this effect will be observed in a modality other than visual such as auditory. In addition, a research of multisensory interaction is also interesting to investigate the mechanism of time perception. For example, will an auditory stimulus magnitude of which changes continuously affect temporal processing of a visual stimulus that followed?

In the experiment of Chapter 4, one of the possible future researches is to change reference intervals into sub-second range. It is suggested that the different neural networks were engaged in processing of sub and supra second ranges (Lewis & Miall, 2003b). In sub-second range, SMA and the basal ganglia activated irrespective of modalities (auditory or visual) and stimuli structures (empty or filled interval) that were used at the temporal tasks (Shih *et al*., 2009). These differences of activation pattern between sub- and supra- second ranges may lead results that will be different from the result in this thesis.

Another one is to investigate how the speed of internal clock changes depending on the mode of motor control more concretely by using temporal order judgment or simultaneity judgment. When the speed of internal clock becomes faster (slower), an interpulse interval becomes shorter (longer). Since it is thought that multiple events that are dropped into between successive two pulses are perceived simultaneously, performances of temporal order and simultaneity judgment for these events will be worse. On the contrary, when timings of multiple events are put across successive pulses, it is thought that we will perceive them in succession and non simultaneous. The slower the internal clock becomes, the wider the interval between pulses becomes. Therefore, performances of temporal order and simultaneity judgments will be worse when the clock rate becomes slower.

In addition, it is possible to combine the experimental paradigms in this thesis. For example, pressing a button will induce a sensory stimulus the magnitude of which changes gradually. The subject estimates its interval. When the mode of movement of pressing a button change as the

experiment in chapter 4, will the temporal processing of the stimulus that changes its magnitude gradually be affected?

Moreover, in order to understand the mechanism of subjective time further, I think that one of the possible research directions is to focus on common and different mechanisms between motor and perceptual temporal processing in the brain. As described above, it is thought that there were some relations between the temporal processing of motor and perception. Since both motor and perception have temporal aspects, it might be possible that some common neural mechanisms, if any, between motor and sensory cortex may contribute to construct subjective time. If effects of various factors such as aging and arousal on temporal processing differs between motor and perception, a property of neural mechanism that correlates with these effects might be a candidate which is engaged in time perception. On the contrary, if there is a clear difference of temporal processing between perception and motor, it may be attributed to the anatomical differences between them. If so, it would be possible to study subjective time from a morphological and an anatomical perspectives.

In this thesis, I mainly focused on subjective duration, but subjective timing is also one of the important aspects of subjective time. A neural mechanism that determines a perceived timing of various mental events such as sensory stimulus, action, emotion, and intention is still unclear. Perceived timings of these events are not straightforward with the external objective temporal axis. Perceived temporal order and interval of successive events are important for a sense of agency. The sense of agency is feeling that oneself is the agent of one's own action.

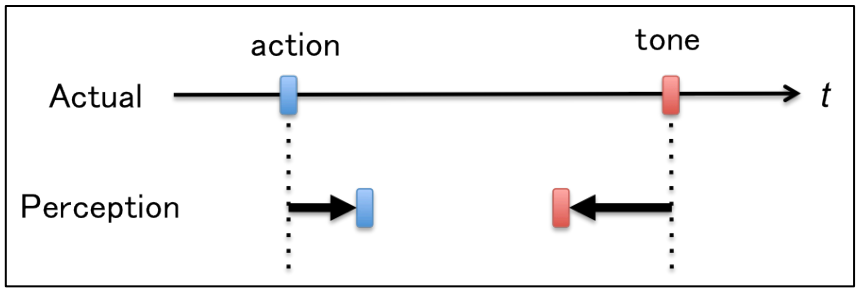


Figure 5.1 Intentional binding effect. A subject presses a key (blue) and it causes a sound tone (red). A delay (a few hundred milliseconds) is inserted between the action and the tone. Perceived timings of the action and the tone are shifted to close each other.

The sense of agency affected perceived timing of an action and sensory stimulus which was induced by the action. As described in Chapter 4, Haggard *et al*. (2002) found that intention to move induced the temporal attraction effect of perceptual timings of action and its sensory consequence (intentional binding effect). In their study, a subject pressed a key voluntarily and it caused a sound tone 250 ms after the key pressing. The subject judged the timing the action or the tone happened. The timing of the action and the tone the subject perceived were shifted to close each other (i.e., the perceived timings of the action and the tone shifted forward and backward, respectively). On the other hand, when TMS made the subject induce an action involuntarily, perceived timing of action and its sensory consequence shifted to a direction for getting away each other. The magnitude of binding was affected by probability of occurrence of sensory feedback (Moore & Haggard, 2008). Ebert and Wegner (2010) showed that sense of authorship was one of the factors that affected the magnitude of intentional binding effect. Emotion also affected the binding effect, in which when sensory feedback of action was an emotional negative sound, the binding effect decreased compared to a positive one (Yoshie & Haggard, 2013).

The studies also showed that higher cognitive mechanism might engage in the intentional binding effect. A subject who was primed low power showed less temporal attraction effect than a high power primed subject (Obhi *et al*., 2012). A moral responsibility for an outcome of one's own choice affected the intentional binding effect (Moretto *et al*., 2011). When a type of sensory feedback represented value of rewards, the magnitude of temporal binding effect was depending on its reward (Takahata *et al*., 2012). The negative outcome reduced temporal attraction shift. Other study showed that a level of physical effort such as pulling a stretch band also affected magnitude of intentional binding. The higher level of physical effort induced larger binding effect than the lower level of physical effort (Demanet *et al*., 2013). These results suggested a higher mechanism engaged in constructing subjective time.

Stetson *et al*. (2006) gave an alternative hypothesis for the intentional binding and tested it. They hypothesized that there existed motor and sensory temporal axes independently. The brain arranged these two temporal axes to maintain action-effect causality. Thus, if a delay is inserted between an

action and its sensory feedback, the brain recalibrates the arrangement of axes to become sensory feedback happened after action without the delay as usual. This hypothesis predicted that after this recalibration occurred, a subject would perceive sensory feedback happening before action if the delay between action and sensory stimulus shortened unexpectedly. This phenomenon was actually observed. These studies about subjective timing should be connected to the studies about subjective duration for comprehensive understanding of the mechanism of subjective time.

The researches of subjective time are also important for the study of free will. The experiment showed that neural activity for action initiation began unconsciously before conscious intention to move occurred (Libet *et al*., 1983). In their task, a subject performed a flexion of the fingers and/or the wrist of the hand. The action the subject performed was spontaneous self-initiated movement (i.e., the subject did not preplan when to move). The subject watched a clock where a spot of light rotated as a clock hand and answered the position of the spot that she or he wanted to move and actually moved. Libet *et al*. (1983) used the readiness potential measured by EEG as an indicator for beginning of voluntary movement. The readiness potential is a negative electrical activity of the brain that begins and increases gradually about 800 ms before voluntary movement is initiated (Kornhuber & Deecke, 1965). The Libet's experiment showed that the activity of readiness potential began before the timing at which the subject reported she or he had wanted to move. The average timing of initiation of readiness potential was about 550 ms before the movement. The estimated timing of intention to move averaged about 200 ms before the movement. Therefore, the activation of brain began about 350 ms before the subject intended to move consciously. This result has been one of the evidences against our possession of free will. However, the task they used was complex (attending own intention was unnatural situation) and depended on the subject's memory. Subjective time is a complex phenomenon and dynamically changes as described so far. Therefore, there is a possibility that something undiscovered mechanism might engage in this phenomenon. Lau *et al*. (2004) showed that, using Libet's paradigm, when a subject attended to their intention to move, pre-SMA was activated. Pre-SMA was also the area when a subject engaged in temporal timing task. Therefore, it might be possible that there is an interaction between subjective time and intention to move.

The studies of subjective time might be able to contribute a series of the studies about free will by providing a new paradigm. Matsuhashi and Hallett (2008) used a new method to investigate the temporal relation between the initiation of the readiness potential and the intention to move. Their method did not depend on a recall of event by a subject such as Libet's paradigm. The result showed that the estimated timing at which intention to move occurred was about 1.42 s before the action. Although the initiation of the readiness potential preceded the intention to move as Libet's experiment, the timing of intention to move in the study of Matsuhashi and Hallett (2008) was earlier about 1.2 s than that of Libet *et al*. (1983). The large difference between these studies indicates that it needs a more sensitive method to measure a timing of mental event. In addition, a situation of experimental task should be set up as natural as possible. Attending to intention to move is unnatural situation in real life and it might result in an incorrect conclusion. By using of the result and methods of the studies of time perception so far, it will able to provide a better method in order to measure the timing of intention to move more accurately.

One of the interesting researches is to investigate a relation between the readiness potential and subjective time. A study showed that when preparing to initiate action, subjective time dilated and temporal resolution was enhanced (Hagura *et al*., 2012). This result was different from the other studies about time perception in which subjective duration expanded but temporal resolution did not change such as the study of the effect of emotion (Droit-Volet & Meck, 2007). Although the study of Hagura *et al*. (2012) did not measure EEG, it might be possible that readiness potential have a role in subjective time to some extent.

Perceived magnitude of sensory feedback by one's own action is attenuated compare to the same magnitude of sensory stimulus made by others (Shergill *et al*., 2003). One of the familiar examples is that a person cannot tickle oneself. The study showed inserting delay between an action and its sensory feedback by an apparatus can induce a sensation of tickling by one's own action (Blakemore *et al*., 1999). One of the models that explains about this phenomenon is the internal forward model (Wolpert *et al*., 1995) (Figure 5.2). The internal forward model suggested that motor command generates an efference copy of motor action in addition to a motor signal that actually induces motor output. The efference copy is used for a prediction of a consequence of the motor output. This

prediction is compared with an actual sensory input. If the actual sensory feedback matches the prediction, perceived magnitude of the sensory stimulus is attenuated. If this model coincides with reality, it indicates that the brain has an ability to calculate and predict an interval between the motor output and the its sensory consequence. The brain is also able to estimate an actual delay between motor output and its feedback. In addition, there is a neural mechanism that compares the predicted delay with the actual delay. This function is not simple since the interval between action and feedback is not always constant. The quicker a person move, the earlier its sensory feedback comes. The delay between motor output and its feedback is different depending on the body parts. For instance, the delay of moving the finger of the foot is longer than that of the hand. The brain should deal with these variations of the delays.

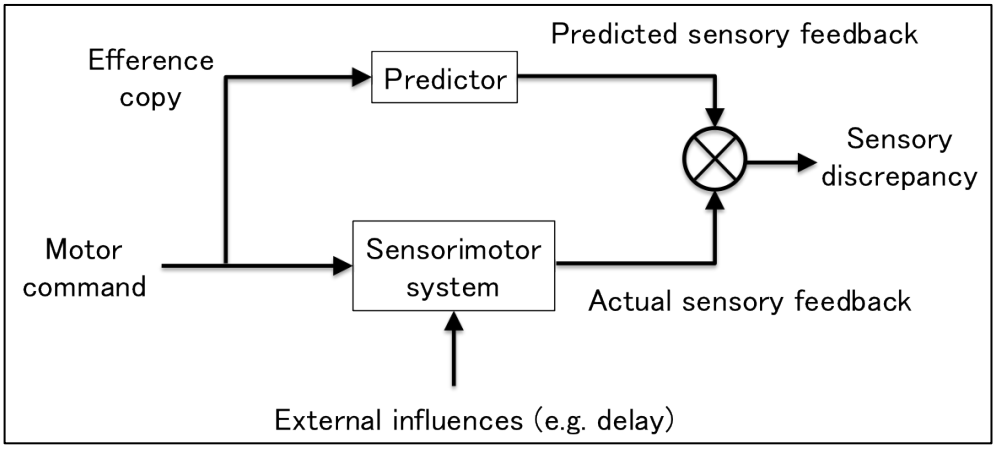


Figure 5.2 Diagram of internal forward model. Adapted from Blakemore *et al*. (1999).

Libet (2004) suggested "time-on theory" which indicated that continuous neural activity for 500 ms is needed to perceive a near threshold sensory stimulus consciously. The results of studies about the time-on theory are important because they showed that the relation between neural activity and subjective perceived timing of a sensory stimulus. One of the research interests is how the time-on theory will be associated with subjective duration. Further research of the time-on theory also may provide a different approach to subjective time and a novel model of time perception other than the internal clock model.

In summary, our subjective time is constructed dynamically as being affected by the contexts of both perception and motor immediately before. The understanding of these properties of subjective time is useful for applying to engineering and might contribute enhancing quality of our daily life. In order to understand the mechanism of subjective time completely, extensively research will be needed.

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