

博士論文

Psychophysical and neural properties of
context-dependent duration perception

（文脈依存的な時間長知覚における
心理物理学的及び神経科学的特性）

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General Introduction

Time is a fundamental concept that defines our entity. We live in an apparently irreversible flow of time, from the past through the present to the future, and our conscious experience is associated with the order or length of time. Time has created extensive interest in various fields including philosophy, art, and science, however, the definition of “time” has been quite diverse across fields. For example, Gibson (1979) described the difference between the physical and perceptual time as follows:

[...] the flow of ecological events is distinct from the abstract passage of time assumed in physics. The stream of events is heterogeneous and differentiated into parts, whereas the passage of time is supposed to be homogeneous and linear. [...] Events are perceived, but time is not.

In line with Gibson’s conceptual framework that what we perceive as “time” is the flow of ecological events, not the physical time, psychological investigations of time have revealed that the temporal processing in different timescales is indeed related to specific ecological functions and controlled by corresponding neural mechanisms (Figure 0.1). When researchers focus on the “perception” of event duration, it often refers to a duration of hundreds of milliseconds to seconds (Allman, Teki, Griffiths, & Meck, 2014).

When we time the duration of events in the external world, the temporal information is given through sensory systems. However, the sensory information available for organisms is sometimes too impoverished to make appropriate decisions (Ma & Jazayeri, 2014). Many psychophysical studies have indicated that the timing system utilizes various clues to optimally estimate the event duration. For instance, spatial and temporal frequencies of a stimulus (Aen-Stockdale, Hotchkiss, Heron, & Whitaker, 2011; Kanai, Paffen, Hogendoorn, & Verstraten,

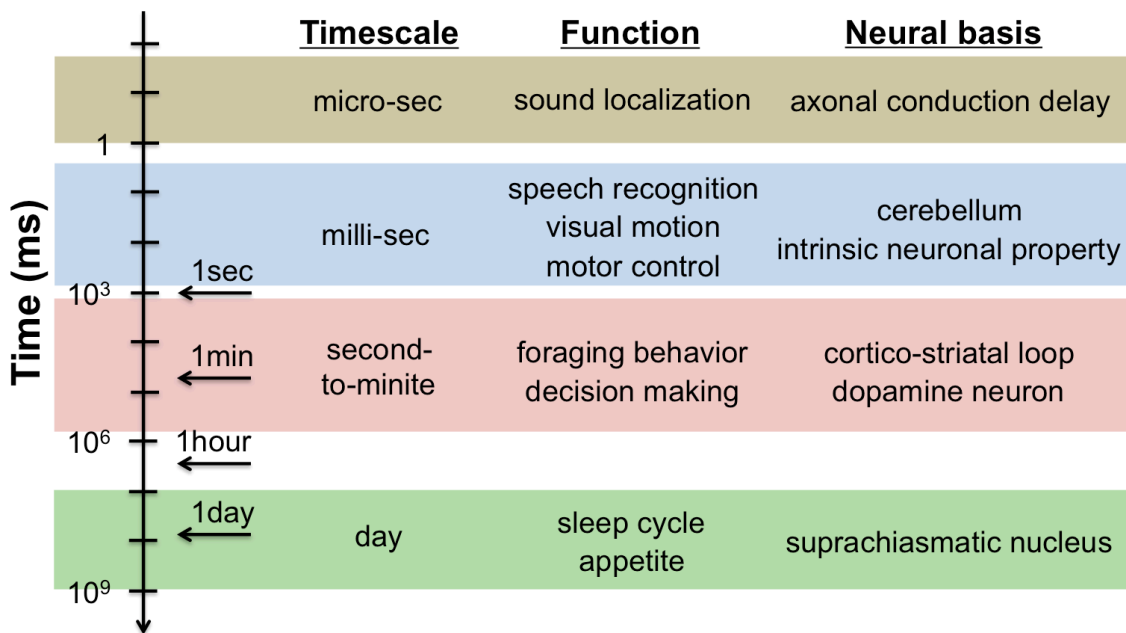


Figure 0.1. Timescales of temporal processing. Adapted from Buhusi & Meck (2005) and Mauk & Buonomano (2004). Temporal information in different timescales is related to different behavioral functions, and processed by different neural mechanisms.

2006; Kaneko & Murakami, 2009), eye movements (Morrone, Ross, & Burr, 2005), attention (Mattes & Ulrich, 1998; Tse, Intriligator, Rivest, & Cavanagh, 2004), emotional events (Droit-Volet, Fayolle, Lamotte, & Gil, 2013), and working memory load (Fortin & Breton, 1995) have all shown to influence the perceived duration of a stimulus or an event. In particular, considerable research has focused on how the temporal context modulates the perception of duration (for reviews, see Bausenhardt, Bratzke, & Ulrich, 2016; Shi & Burr, 2016; Shi, Church, & Meck, 2013).

Generally, context effect is a perceptual or cognitive phenomenon that the context

(environmental factors) temporally or spatially proximal to an event affects how the event is perceived. In a classical presentation of the context effect, Bruner & Minturn (1955) demonstrated that an ambiguous figure is recognized differently depending on the context (Figure 0.2). They used an ambiguous figure called “Broken-B” that can be recognized as either the letter “B” or the number “13”, and the subjects answered whether they recognized it as “B” or “13”. A series of letters or numbers was presented prior to the target “Broken-B”, and the subjects recognized “B” after the letter presentation and “13” after the number presentation.

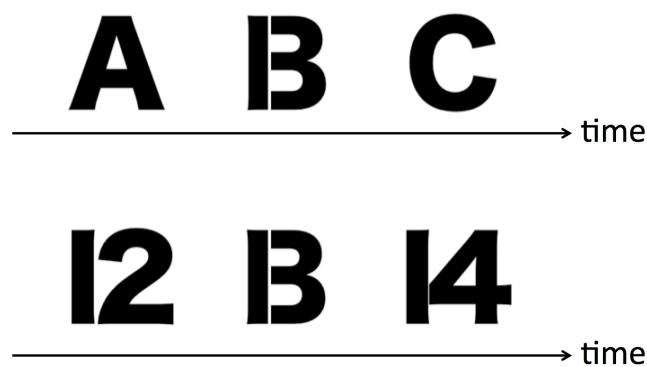


Figure 0.2. An example of the context effect. Made in reference to Bruner & Minturn (1955). The middle “Broken-B” figure is recognized as either “B” or “13” depending on temporally proximal stimuli.

Temporal context effects have also been reported in the field of duration perception. Vierordt's Law is a representative example of how contextual information can influence temporal processing. According to Vierordt's Law, when stimuli with various durations are intermixedly presented, longer durations are underestimated and shorter durations are

overestimated (Lejeune & Wearden, 2009). One predominant explanation for this phenomenon is Hollingsworth's (1910) central tendency of judgment, in which the perception of time elements in a series is biased toward the mean of that series (Hollingsworth, 1910). Recent computational modeling studies have suggested that the central tendency reflects the optimal encoding process of duration (Acerbi, Wolpert, & Vijayakumar, 2012; Jazayeri & Shadlen, 2010; Ma & Jazayeri, 2014). Because the sensory measurement of an event duration may be noisy and unreliable due to sensory noises, the brain encodes event duration by taking into account the knowledge about temporal statistics in the environment, that is, the knowledge about how long events have occurred in the past.

In this thesis, I studied psychological and neural mechanisms for the optimal encoding process of event duration. In Study 1, I psychophysically investigated how stimulus modality and timescale affect the central tendency, and demonstrated that the central tendency occurs modality-dependently for durations in the sub-second (i.e., hundreds of milliseconds) range, and modality-independently for durations in the supra-second (i.e., several seconds) range. In Study 2, I examined the neural implementation of the optimal duration encoding by using fMRI, and found the activity of timing networks in the brain is plastically modulated depending on previously presented durations.

Study 1:

Timescale- and Modality-dependence of the Central Tendency in Duration Perception

Introduction

Perception of event durations in the external world is vital for many human behaviors (Buhusi & Meck, 2005; Mauk & Buonomano, 2004). However, timing behavior is often susceptible to perceptual noise and decision uncertainty. Indeed, many psychophysical studies have indicated that timing systems use various clues to optimally estimate stimulus durations (Johnston, Arnold, & Nishida, 2006; Tse et al., 2004). In particular, a considerable number of researches have focused on examining how duration perception relies on temporal and non-temporal contextual information, such as previously presented durations and sensory modality, respectively (Shi & Burr, 2016; Shi, Church, et al., 2013).

As described in the General Introduction, the central tendency is a representative example of the context-dependent duration perception. Several psychophysical studies have revealed that the magnitude of the central tendency differs substantially between individuals, and investigated which components of the timing system mediate these individual differences (Cicchini, Arrighi, Cecchetti, Giusti, & Burr, 2012; Malapani et al., 1998). Studies that use computational modeling have shown that the central tendency is associated with timing precision; the noisier the internal representation of the duration, the larger the central tendency (Acerbi et al., 2012; Jazayeri & Shadlen, 2010). As described below, timing precision may depend on various factors, including sensory modality and the length of the timed stimulus.

A traditional but widely accepted model for duration perception in the millisecond-to-second range is the pacemaker-accumulator model. This model assumes the presence of a modality- and timescale-invariant central clock (Treisman, 1963). The scalar property also assumes that timing precision, defined as the ratio of the standard deviation of the

perceived duration to the stimulus duration, is constant in the millisecond-to-second range, and is a prominent finding in the field of time perception (Gibbon, 1977; Keele, Pokorny, Corcos, & Ivry, 1985). Furthermore, recent modeling studies also suggest the presence of a modality- and timescale-independent timing system (Rammsayer & Troche, 2014; Stauffer, Haldemann, Troche, & Rammsayer, 2012). In contrast, many psychological studies have indicated that timing precision does depend on the sensory modality (Cicchini et al., 2012) and timescale (Gibbon, Malapani, Dale, & Gallistel, 1997; Hayashi, Kantele, Walsh, Carlson, & Kanai, 2014). Durations in the sub-second (i.e., hundreds of milliseconds) and supra-second (i.e., several seconds) ranges are involved in different behavioral functions, and therefore recruit different neural mechanisms (Buhusi & Meck, 2005). Previous psychological studies have reported that the coefficient of variation or the Weber fraction of the perceived duration changes at the boundary at around 1 second (Gibbon et al., 1997; Grondin, 2014), and that cognitive load affects differently for the sub- and supra-second timing performance (Rammsayer & Lima, 1991). Neuroimaging studies have also demonstrated that there are two timing networks in the brain divided by a boundary of approximately one second (Lewis & Miall, 2006; Wiener, Turkeltaub, & Coslett, 2010). Moreover, several computational models include sensory modality dependent components, especially for sub-second timing, such as time-dependent changes in the state of the neural network (Buonomano & Maass, 2009; Karmarkar & Buonomano, 2007), or time-sensitive mechanisms in early sensory processing (Heron et al., 2012; Johnston et al., 2006). In line with these studies, Cicchini et al. (2012) found that visually defined sub-second durations induced a larger central tendency than auditorily defined sub-second durations due to the higher temporal precision of the auditory modality. Whether

such modality-dependent variations in the central tendency occur for supra-second durations is still a matter of debate (Noulhiane, Pouthas, & Samson, 2009; Ryan, 2011).

The present study aimed to examine how stimulus modality affects the optimal encoding of time across different timescales. If the source of timing noise is located at modality-dependent timing mechanisms, then the central tendency for visual and auditory durations should occur independently. If a common modality-independent timing mechanism is also involved in the central tendency, then the central tendencies for the visual and auditory modalities should show within-individual correlations. I hypothesized that the central tendency occurs differently for auditory and visual timing in the sub-second range and depends on modality-dependent processing, whereas a common modality-independent timing system regulates the central tendency in the supra-second range. To test these hypotheses, I quantified the central tendency for visual and auditory timing in the sub- and supra-second ranges.

In Experiment 1, I investigated how stimulus modality and timescale affect individual differences in the central tendency. In Experiment 2, I examined whether modality-dependent time encoding in the sub-second range results from differences in temporal sensitivity between the visual and auditory systems by controlling for differences in the discrimination of durations in the sub-second range between the two modalities.

Experiment 1

Methods

Participants

Twenty healthy volunteers (13 males and 7 females, 18–29 years old) participated in

Experiment 1. All participants gave written informed consent for their participation in the experiment, which was approved by the institutional review board at The University of Tokyo. All participants reported to have normal hearing and normal or corrected-to-normal vision.

Apparatus

The auditory stimuli were presented through an Audio Stream Input/Output (ASIO) compliant USB digital-to-analog converter (Roland UA-1G) and SONY MDR-XB500 headphones at 60 dB. The visual stimuli were presented on a CRT monitor (Mitsubishi Electric RDF223H, 1024 × 768 pixels, 120 Hz refresh rate). Participants were seated 57.3 cm from the monitor in a dark soundproof room; participants' heads were stabilized using a chin rest.

Stimuli and procedure

Stimuli were generated using MATLAB (MathWorks, R2012b) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). A schematic of the task is shown in Figure 1.1. In the task, a pair of stimuli was briefly presented, one after the other. The visual stimulus was a white disk (5 degrees in diameter), while the auditory stimulus was a simple tone (600Hz, 60dB). Participants were asked to reproduce durations between the pair of stimuli by pressing a button with the forefinger of their dominant hand. Participants were instructed not to count the duration between stimuli (Rattat & Droit-Volet, 2012). Each visual flash or auditory tone lasted for 20 ms. A cosine ramp of 5 ms was applied to the onset and offset of all auditory stimuli. Stimulus durations were either sub-second or supra-second. The sub-second durations were 400–600 ms with 50 ms steps. The supra-second durations were 2000–3000 ms with 250 ms steps; the supra-second durations were scaled 5 times longer. The inter-trial intervals (ITI) ranged from 1.2 s to 1.8 s.

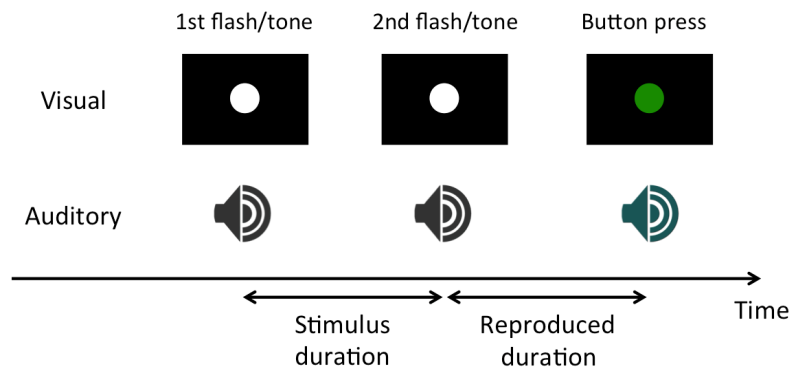


Figure 1.1. Schematic of the experimental procedure. Two brief flashes or tones were sequentially presented, and participants made button presses to reproduce the duration. Correct or incorrect feedback was presented immediately after participants' responses.

Immediately after the subject's response, a sensory feedback was given in every trial. If the reproduced duration was within a certain time frame of the actual duration, the same stimulus (i.e. a white disc or 600 Hz tone) was presented as positive (correct) feedback; otherwise, a green disk or a 400 Hz tone was presented as negative (incorrect) feedback. Each sensory feedback lasted for 20 ms. To compensate for the scalar property, the ratio of the width of this feedback time window to the stimulus duration was kept constant across the different stimulus durations. This feedback ratio was adaptively controlled using a one-up, one-down staircase method that adds or subtracts 0.015 for each incorrect or correct trial, respectively (Jazayeri & Shadlen, 2010).

Participants completed 4 separate experimental blocks, each of which was one of the 4 combinations of sensory modalities and timescales (i.e., visual sub-second, auditory sub-second, visual supra-second, auditory supra-second). At the beginning of each block,

participants completed a practice session with 50 trials in order to become accustomed to the timescales and modalities. After the practice session, participants completed a total of 200 trials in each block. Each block was divided into 2 sessions for sub-second conditions, or 4 sessions for supra-second conditions. The presentation order of durations within a session was randomized. The order of blocks was also randomized across participants using a Latin square method. Participants completed all 4 blocks twice by coming in on two separate experimental days. In total, 400 trials were completed for each timescale-modality condition.

Analysis

Trials in which the reproduced duration deviated more than 3 standard deviations (SDs) from each condition's mean were excluded from all analyses. I linearly regressed the reproduced duration to the stimulus duration for each individual. The slopes of the linear regressions were compared across conditions as indices of the central tendency. For example, if stimulus durations were reproduced accurately then the slope was 1. However, if the central tendency occurred and longer durations were underestimated and shorter durations overestimated, the slope values were less than 1. To examine how stimulus modality and timescale affect the central tendency, I conducted a two-way repeated-measures ANOVA with stimulus modality (visual or auditory) and timescales (sub- or supra-second) as factors. Furthermore, I calculated within-individual correlations of the central tendency across different sensory modalities and timescales, in order to investigate whether modality- and timescale-independent timing systems are involved in the central tendency.

Results and Discussion

Figure 1.2 shows the reproduced durations in each condition. Overall, the central tendency was observed at a group level in all of the conditions except the auditory sub-second condition, as shown in previous studies (Cicchini et al., 2012; Ryan, 2011).

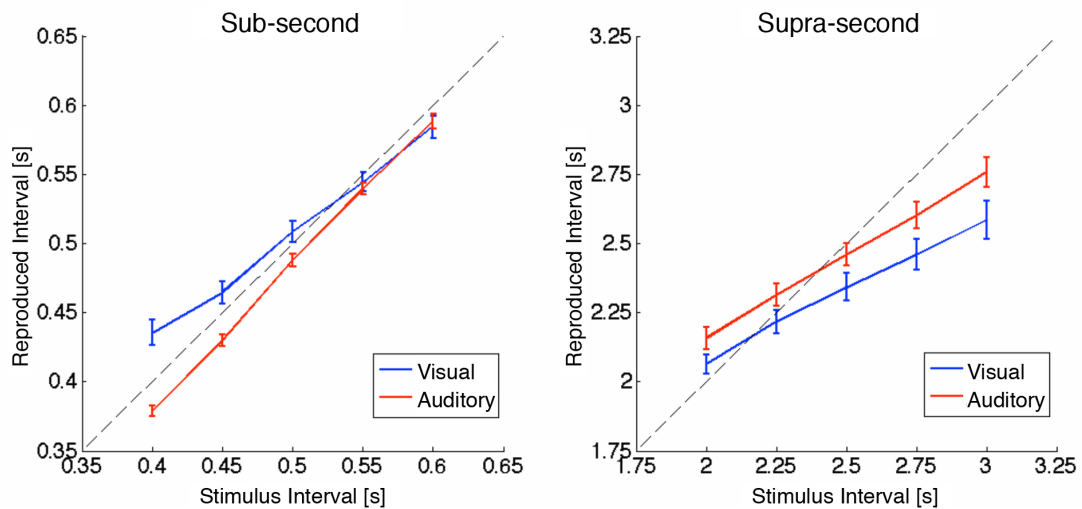


Figure 1.2. Group means of the reproduced durations. The left panel indicates the results for sub-second timing. The right panel indicates the results for supra-second timing. Blue lines represent results for visual stimuli, and red lines represent results for auditory stimuli. Dotted lines correspond to accurate reproduction of the stimulus durations. Error bars represent the standard error of the mean.

Figure 1.3 shows the magnitude of the central tendency in each condition. A two-way repeated-measures ANOVA revealed significant main effects of the stimulus modality ($F(1,76) = 17.5, p < .001$) and timescale ($F(1,76) = 55.8, p < .001$), as well as a significant interaction ($F(1,76) = 9.20, p = .003$). These results indicate that (1) the visual modality is more

susceptible to the central tendency, (2) the magnitude of the central tendency is larger in the supra-second range, and (3) the difference in the magnitude of the central tendency between visual and auditory durations is larger in the sub-second range. As shown in Figure 1.3, the magnitude of the central tendency was significantly different between the visual and auditory modalities for sub-second timing ($t(19) = 6.14, p < .001$), but not supra-second timing ($t(19) = 2.16, p = .087$, Bonferroni-corrected; the Bonferroni corrections were applied for two comparisons).

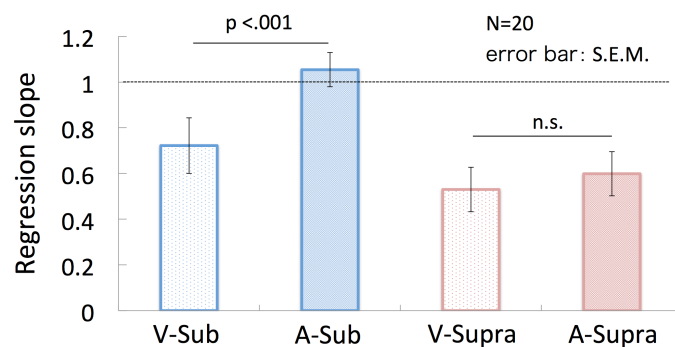


Figure 1.3. Quantification of the central tendency. The slopes of the linear regressions are presented for all four conditions. A and V represent auditory and visual stimuli, respectively. Sub and sup represent sub-second and supra-second durations, respectively. Error bars represent the standard error of the mean. n.s. = not significant.

I further examined within-individual correlations of the central tendency across modalities and timescales. The magnitudes of the central tendency for the visual and auditory modalities were significantly correlated for supra-second timing ($r = .86, p < .001$,

Bonferroni-corrected), but not sub-second timing ($r = .35$, $p = .25$, Bonferroni-corrected; Figure 1.4a). However, as shown in Figure 1.4b, the magnitudes of the central tendency for sub- and supra-second durations were not correlated for the visual modality ($r = .48$, $p = .12$, Bonferroni-corrected) or the auditory modality ($r = .09$, $p = .99$, Bonferroni-corrected; the Bonferroni corrections were applied for four comparisons). These results indicate that a modality-dependent component of the timing system is responsible for the central tendency in the sub-second range, while a common modality-independent timing system influences the central tendency in the supra-second range.

Because the reproduction task required motor responses, the reproduced durations and corresponding analyses might be susceptible to motor noise. Wearden (2003) suggested that the motor noise lead a noisier variability of reproduced durations for relatively shorter durations (Wearden, 2003). This noise could thus make the estimates of the central tendency more unreliable for the relatively shorter sub-second durations. One might argue that the non-significant correlation of the sub-second central tendency between modalities could be attributed to these noisy and unreliable estimates of the central tendency. To test whether the results obtained in the sub-second range were reliable, I examined whether task performance in the first and second experimental days were correlated in each condition. The magnitude of the central tendency in the first and the second experimental days were significantly correlated in all conditions (Table 1.1). These results suggest that the magnitude of the central tendency is stable within individuals across different experimental days, and reliably estimated in all conditions, including the sub-second durations.

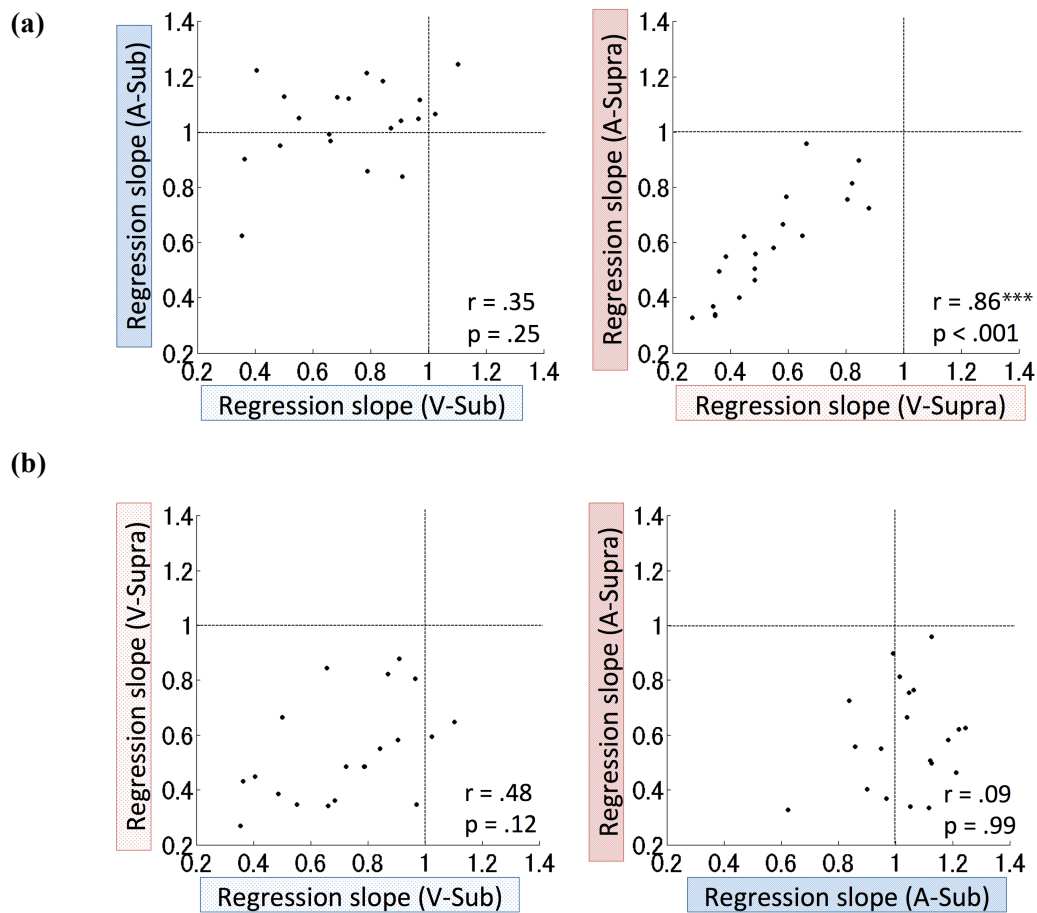


Figure 1.4. Within-individual correlations of the central tendency across different sensory modalities (a) and timescales (b). Regression index represents the slope of the linear regression of the reproduced durations to the stimulus durations. Each small circle represents an individual's data. V and A stand for the visual and auditory conditions, respectively. Sub and supra represent the sub-second and supra-second durations, respectively. *** $p < .001$.

Table 1.1. Correlations between the magnitudes of the central tendency on the first and second experimental days.

Condition	Correlation coefficient	P-value
V-sub	.74	.003
A-sub	.71	.006
V-supra	.64	.010
A-supra	.66	.013

Note. V and A stand for the visual and auditory modalities, respectively. Sub and supra represent the sub-second and supra-second durations, respectively. P-values were Bonferroni-corrected for four comparisons.

Similar to Cicchini et al.'s study, I observed a significant central tendency for the visual but not the auditory sub-second durations. However, some participants in the present study, as well as in Cicchini et al.'s study, exhibited the central tendency for auditory sub-second durations. One possible explanation for this finding may be the presence of individual differences in sensory precision across modalities. Temporal resolution in the auditory modality is generally finer than in the visual modality, although such auditory superiority is not always observed (Kuroda, Hasuo, Labonte, Laflamme, & Grondin, 2014). If the deviation of the internal representation of a stimulus duration is too small to overlap neighboring durations, the perceived duration for that stimulus might not be affected by neighboring durations. In both Cicchini et al.'s study and the present investigation, the spacing

between stimulus durations was the same for the auditory and visual modalities, and was not normalized by the specific timing precision across individuals or sensory modalities. Therefore, in Experiment 2, I examined whether the modality-dependent central tendency in the sub-second range resulted from differences in the temporal sensitivity between the visual and auditory systems by controlling for differences in the discrimination of sub-second durations between the two modalities.

Experiment 2

Methods

Participants

Thirteen healthy volunteers (7 males and 6 females, 19–30 years old) participated in Experiment 2. All participants gave written informed consent for their participation in the experimental protocol, which was approved by the institutional review board at The University of Tokyo. All participants reported to have normal hearing and normal or corrected-to-normal vision.

Apparatus

The auditory stimuli were presented through an Audio Stream Input/Output (ASIO) compliant USB digital-to-analog converter (Roland UA-1G) and SONY MDR-XB500 headphones at 60 dB. The visual stimuli were presented on a CRT monitor (Mitsubishi Electric RDF223H, 1024 × 768 pixels, 120 Hz refresh rate). Participants were seated 57.3 cm from the monitor in a dark soundproof room; participants' heads were stabilized using a chin rest. All apparatuses were the same as in Experiment 1.

Stimuli and procedure

Stimuli were the same as in Experiment 1. Visual stimuli were white disks, while auditory stimuli were pure tones (600 Hz).

Experiment 2 consisted of a discrimination task and a reproduction task. The discrimination task was first conducted to normalize individual differences in temporal discriminability across the visual and auditory modalities. In the discrimination task, three successive flashes or tones that marked two neighboring durations were presented, and participants reported whether the first duration was longer or shorter than the second. The standard duration was always 500 ms, while the comparison durations ranged from 350 ms to 650 ms with 50 ms steps. All comparison durations were presented 32 times. The order of the standard and comparison durations was randomized across trials. The visual and auditory durations were tested in separate sessions. In the analyses, the probability at which the participant judged the comparison to be longer than the standard was plotted as a function of the comparison duration. The discrimination sensitivity was calculated by fitting a cumulative normal function as a psychometric function. The discrimination sensitivity was defined as the Weber fraction. Weber fractions were defined as the ratio of the just noticeable difference (JND; half of the difference between the durations giving 25 % and 75 % of the psychometric function) to the standard duration (JND/500). Discrimination sensitivities for the visual and auditory durations were separately estimated for each participant.

For each participant, the reproduction task followed the discrimination task in the same modality. The order of visual and auditory tasks was randomized across participants. Durations used in the reproduction task were determined for each participant and for each

stimulus modality based on the participant's performance in the discrimination task. To be precise, durations that gave 20, 35, 50, 65, and 80 percentiles in the psychometric function were used. Accordingly, all participants performed the visual and auditory tasks with physically different but perceptually the same durations.

As in Experiment 1, correct and incorrect feedback was given after each trial in the reproduction task. If the reproduced duration fell within a certain time frame of the stimulus duration, correct feedback was presented; otherwise, incorrect feedback was presented. In contrast to Experiment 1, the ratio of the width of the feedback time frame of the stimulus duration was also normalized for each participant. The feedback ratio was adaptively controlled with a one-up, one-down staircase method that added or subtracted 15 % of the Weber fraction, for each incorrect or correct trial, respectively.

Trials in which the reproduced duration deviated more than 3 SDs from each condition's mean were excluded from all analyses. As in Experiment 1, the reproduced durations were linearly regressed to the stimulus duration, and the slopes of the linear regressions were compared across modalities as indices of the central tendency (Cicchini et al., 2012; Levy, Namboodiri, & Hussain Shuler, 2015).

Results and Discussion

To estimate discrimination sensitivity, I first drew psychometric functions for each participant and for each stimulus modality (Figure 1.5). Two participants were excluded from subsequent analyses because their response for either the shortest or the longest comparison duration did not reach 20 or 80 % respectively in both modalities. The Weber fractions were

0.145 ± 0.036 for visual stimuli and 0.126 ± 0.046 for auditory stimuli. There was no significant difference between the Weber fractions of visual and auditory durations ($t(10) = 1.90, p = .09$).

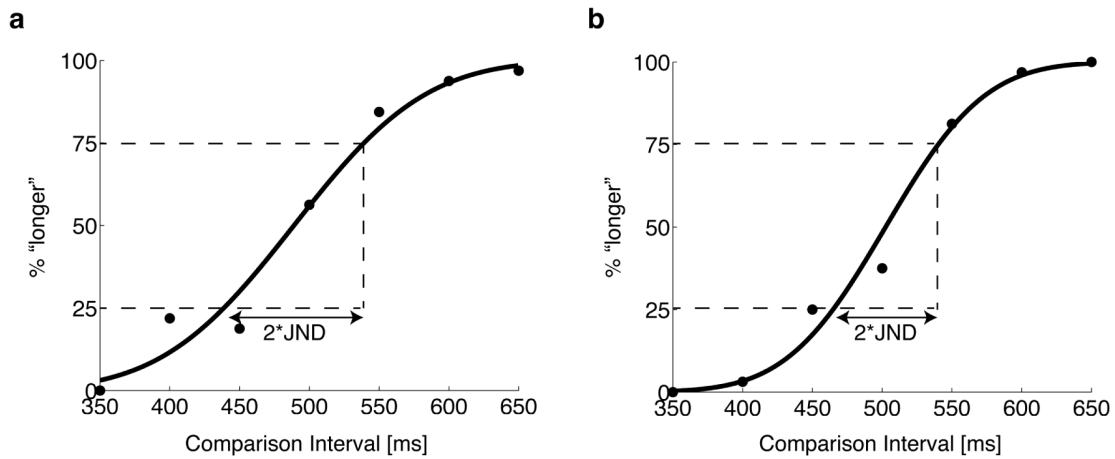


Figure 1.5. Psychometric functions of visual (a) and auditory (b) durations for a typical subject. The probabilities at which the subject judged that the comparison (350-650 ms) was longer than the standard (500 ms) were plotted, and fitted to the cumulative normal distribution function. The discrimination sensitivity was defined as the Weber fraction, the ratio of the just noticeable difference (JND) to the standard duration.

In the reproduction task, even though the spacing between stimulus durations was normalized across participants and stimulus modalities by using the discrimination task, the magnitude of the central tendency substantially varied across individuals (Figure 1.6). The magnitude of the central tendency was significantly larger for visual durations than auditory durations ($t(10) = 3.89, p = .003$), as in Experiment 1. Additionally, the magnitude of the central tendency for visual and auditory sub-second durations was significantly correlated ($r = .69, p$

= .018). This result suggests that a common or homologous system is also involved in the optimal encoding of time in both auditory and visual sub-second perception.

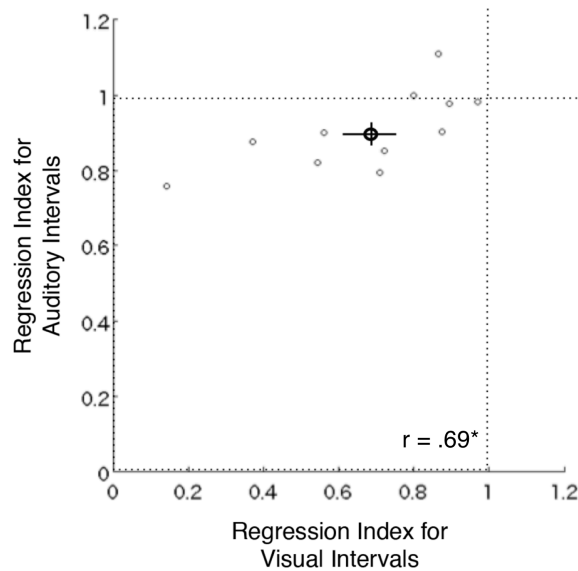


Figure 1.6. Within-individual correlations of the central tendency across visual and auditory modalities. Regression index represents the slope of the linear regression of the reproduced durations to the stimulus durations. Small open circles represent each individual's data. Bold circles and bars represent the mean and the standard error of the mean, respectively. * $p < .05$

In the duration discrimination task, there was no significant difference between the discrimination sensitivities of the visual and auditory modalities (Experiment 2). Kuroda et al. (2014) also reported that the sensitivity of duration discrimination is almost identical for visual and auditory stimuli (Kuroda et al., 2014). Therefore, modality-dependency of the central tendency may not be explained by differences in timing precision between modalities. Because

the time reproduction task requires sensorimotor timing, it is possible that the timing precision of the reproduction task and the discrimination task are independent. However, previous studies indicated that variances of the perceived durations in the reproduction and discrimination tasks are significantly correlated (Merchant, Harrington, & Meck, 2013; Merchant, Zarco, & Prado, 2008). Therefore, it is reasonable to determine stimulus durations in the reproduction task based on performance in the discrimination task.

In Experiment 2, a significant central tendency was also observed for auditory durations ($t(10) = 2.99$, $p = .014$). This result is seemingly inconsistent with results in Experiment 1. One possible explanation for this difference might be the range of stimulus durations. The means and SDs of the differences between the shortest and longest stimulus durations was 182.1 ± 45.5 ms for visual stimuli and 160.6 ± 57.2 ms for auditory stimuli. Therefore, the stimulus durations were narrowly ranged on average compared to Experiment 1, in which the difference between the shortest and the longest stimulus durations was 200 ms. Previous studies have demonstrated that the distribution of stimulus durations affects the memory bias in duration perception (Acerbi et al., 2012; Ryan, 2011; Wearden & Ferrara, 1995). Especially, the present results is consistent with the finding that the narrowly-ranged stimulus durations amplify the central tendency in the auditory modality (Noulhiane et al., 2009). Further study will be needed to investigate how the distribution of stimulus durations modulates the magnitude of the central tendency in relation to the stimulus modality and the duration discriminability.

General Discussion

In the present study, I investigated how stimulus modality and timescale affect individual differences in the central tendency of duration perception. The magnitude of the central tendency differed substantially between individuals, but was stable across different experimental days for each individual. The magnitude of the central tendency greatly varied depending on the timescale and the sensory modality, suggesting that timescale- and modality-dependent timing systems are responsible for individual differences in this phenomenon.

Timescale-dependence of the central tendency

The present results indicate that sub- and supra-second timing influence the central tendency differently. A traditional view according to the scalar property assumes that timing precision, defined as the ratio of the standard deviation of the perceived duration to the stimulus duration, is constant across sub- and supra-second ranges (Gibbon, 1977). If the magnitude of the central tendency depends on timing precision and the scalar property, as suggested by previous studies (Acerbi et al., 2012; Jazayeri & Shadlen, 2010), then the central tendency should occur equivalently for sub- and supra-second timing. Contrary to this traditional view, the current study found that the magnitude of the central tendency was larger in supra-second timing than in sub-second timing. Several psychological studies support this finding and have also demonstrated that timing performance is less precise in the supra-second range compared to the sub-second range (Gibbon et al., 1997; Lewis & Miall, 2009). The larger central tendency in the supra-second range might result from the noisier representation of durations in the supra-second range. In addition to the difference in timing precision between sub- and

supra-second timing, it should be noted that the experimental setting of ITIs might also lead the larger central tendency in the supra-second range. Meck (1985) suggested that the timing performance is impaired when the ratio of the timed duration to the ITI is large (Meck, 1985). In the present study, the same ITIs were used for sub- and supra-second trials. Therefore, the ratio of the timed duration to the ITI was larger in the supra-second, which might lead the larger timing bias in the supra-second range.

The magnitudes of the central tendency in the sub- and supra-second range were not correlated in both modalities (Experiment 1). Therefore, no evidence for the involvement of timescale-independent timing mechanisms in the central tendency was found. This result is consistent with a previous investigation that showed timing precision was not correlated between sub- and supra-second durations (Hayashi et al., 2014). In the present study, stimulus durations within a given session had narrow ranges (i.e., 0.4–0.6 s for sub-second, 2.0–3.0 s for supra-second durations) in order to investigate the difference in the central tendency between sub- and supra-second timing. In contrast, previous studies, including the original work of Vierordt (1868), used wide durations that spanned the sub- and supra-second ranges within an experimental session, and observed overestimation of short sub-second durations and underestimation of long supra-second durations (Lejeune & Wearden, 2009). If the sub- and supra-second timing systems were completely independent, the central tendency would not occur across different timescales, but this was not the case. Rammsayer & Troche (2014) proposed a hierarchical mechanism of duration perception in which a timescale-independent superordinate processing system controls the sub- and supra-second timing mechanisms (Rammsayer & Troche, 2014). Based on the present study, timing precision in the sub- and

supra-second ranges affects individual differences in the magnitude of the central tendency. These noisy duration representations in modality-dependent timing systems may be further processed by the timescale-independent superordinate processing system.

Modality-dependence of the central tendency

In the present study, the central tendency was modality-dependent in the sub-second range, but not in the supra-second range; both modalities exhibited a comparable central tendency in the supra-second range. These results suggest that a common modality-independent timing system regulates the central tendency in the supra-second range, while a modality-dependent timing system has a greater impact on the central tendency in the sub-second range.

A previous study investigated the central tendency in the supra-second range in the visual and auditory modalities, and came to the opposite conclusion that a modality-dependent timing system does impact the central tendency in the supra-second range (Noulhiane et al., 2009). In the central tendency, short durations are overestimated and long durations underestimated, resulting in an “indifference point” where durations are estimated accurately. Noulhiane et al. (2009) found that this “indifference point” was different between the visual and auditory modalities when identical stimulus durations were tested (Noulhiane et al., 2009). In contrast, Ryan (2011) showed that the distortion pattern of reproduced durations was comparable between the visual and auditory modalities (Ryan, 2011). In the present study, I observed high within-individual correlations between the magnitudes of the central tendency in the visual and auditory modalities in the supra-second range. This result strongly suggests the involvement of a common modality-independent timing system that regulates the central

tendency in the supra-second range. However, this result does not necessarily exclude the possibility of a modality-dependent mechanism in the regulation of supra-second duration perception. Consistent with the findings of Noulhiane et al. (2009), I observed that auditory durations were overestimated more than visual durations in the supra-second range. This overestimation of auditory durations suggests there are different “indifferent points” between the visual and auditory modalities, and makes it appear as if the magnitude of the central tendency is different for visual and auditory stimuli. However, this general overestimation of all auditory durations could be independent of the central tendency, which is generally thought to be the result of the overestimation of short durations and the underestimation of long durations. Further investigation is necessary to ascertain how modality-dependent general overestimation occurs in the supra-second timing system.

In the sub-second range, differences in the central tendency between the visual and auditory modalities remained, even when the ability to discriminate durations was controlled across sensory modalities (Experiment 2). Previous studies have shown that auditory modality dominates the time perception for audio-visual stimuli (Burr, Banks, & Morrone, 2009; Ortega, Guzman-Martinez, Grabowecky, & Suzuki, 2014). These studies suggest that the timing system utilizes auditory information for temporal estimation rather than visual, even when the perceptual threshold is equalized across the visual and auditory modalities. In contrast to these studies, the present study suggests that sub-second timing in the auditory modality largely relies on stimulus input, and is less affected by contextual information, such as previously presented durations. However, this does not mean that the auditory sub-second timing is not affected by contextual information. Various studies have indicated that previously presented durations do

affect perceived auditory durations (Gu & Meck, 2011; Wiener & Thompson, 2015; Wiener, Thompson, & Coslett, 2014); furthermore, the present study also observed a significant central tendency for auditory durations in Experiment 2.

Interestingly, I observed a significant correlation in the central tendency between the visual and auditory sub-second durations in Experiment 2, in which the spacing between stimulus durations was normalized across modalities based on timing precision that was measured by the duration discrimination task. Therefore, the modality-independent timing mechanism might also be involved in the central tendency in sub-second timing, in addition to the modality-dependent timing mechanism. Several studies support this conclusion that modality-dependent and modality-independent components influence the sub-second timing system. For example, a psychophysical and modeling study revealed a hierarchical timing mechanism whereby modality-specific processing occurs first, followed by modality-independent processing (Stauffer et al., 2012). An alternative model assumes that temporal information is primarily encoded in the auditory system (Filippopoulos, Hallworth, Lee, & Wearden, 2013; Kanai, Lloyd, Buetti, & Walsh, 2011). In this model, temporal information from all sensory modalities is transformed into an auditory format for temporal processing. These two models are not mutually exclusive, and both are consistent with the present results. Further study is necessary to examine the interaction between sensory modalities.

In summary, the present study suggests that individual differences in the central tendency might be associated with a common modality-independent timing mechanism for supra-second timing, and with both modality-dependent and modality-independent timing

mechanisms for sub-second timing.

Incorporating timescale- and modality-dependent components into computational models of the central tendency

In the present study, I showed that both timescale and modality influenced the central tendency. These findings have important implications for the creation of computational models of the central tendency. Recent computational models have accounted for the central tendency in the context of a Bayesian framework (Acerbi et al., 2012; Jazayeri & Shadlen, 2010). Bayesian models assume that a noisy representation of the current stimulus duration (likelihood) is combined with a prior representation of the probability distribution of the stimulus durations presented within the experimental session. Both the likelihood and the prior determine a posterior distribution of the perceived duration, and participants make responses based on this posterior distribution. Such models have two fundamental assumptions regarding the probability distribution of the likelihood that need to be modified in light of the current findings.

One assumption is that the mean of the likelihood is equal to the stimulus duration. However, previous studies have shown that auditory durations tend to be estimated longer than visual durations (Cheng, Scott, Penney, Williams, & Meck, 2008; Penney, Gibbon, & Meck, 2000), which demonstrates that the perceived duration can be systematically shifted from the physical stimulus duration. In the present study, I also observed overestimation of auditory durations in the supra-second range. Previous Bayesian models cannot account for these constant errors. One possible explanation for the overestimation of auditory durations is that auditory signals drive the internal clock faster than visual signals (Gu & Meck, 2011; Penney et al., 2000). However, the timed durations in the present study were empty intervals that were

defined by two brief sensory events and have no signal during the duration itself for both visual and auditory conditions. Considering the absence of sensory signal during the timed duration, it might be unlikely that the observed overestimation for auditory durations is ascribed to the faster accumulation of the internal clock throughout the timed duration. Another interpretation for the overestimation of auditory durations is that the latency to direct attention to the duration onset might be different between modalities, that is, the auditory signal might grab the attention faster (Grondin, 2010; Penney et al., 2000). Since the likelihood of timed durations could change in either case (Shi, Church, et al., 2013), the modality-dependent constant errors should be explained in the framework of Bayesian models by allowing the mean of the likelihood to shift from the physical stimulus duration.

The other assumption regarding the distribution of the likelihood that should be addressed is the scalar property. Psychophysical studies have reported that the scalar property is violated under certain conditions, and that timing precision changes around one second (Gibbon et al., 1997; Grondin, 2014). Indeed, I revealed that supra-second timing is more susceptible to the central tendency than sub-second timing, suggesting that timing precision is lower in the supra-second range than in the sub-second range. Therefore, caution should be taken when assuming that the scalar property holds for all durations across different timescales. The noise distribution of the likelihood may need to be determined separately for sub- and supra-second durations. Therefore, future studies should explore whether the duration distributions within the same timescale and across different timescales exhibit quantitatively similar central tendencies or not. These approaches will provide the means for identifying sources of timing noise that mediate the central tendency and establish a comprehensive model for the optimal encoding of

time.

The present study demonstrated that the internal representation of time is subject to a context-dependent sensori-motor process that optimally encodes temporal information in a modality- or timescale-dependent manner. Although the present study focused to time reproduction as in previous studies (Acerbi et al., 2012; Cicchini et al., 2012; Jazayeri & Shadlen, 2010; Murai & Yotsumoto, 2016), the central tendency has been reported also for duration tasks without motor responses (Gu & Meck, 2011; Wiener & Thompson, 2015; Wiener, Thompson, & Coslett, 2014). Furthermore, Petzschner and her colleagues indicated that we have a common Bayesian principle for optimal magnitude estimation such as movement distance, stimulus length, and also duration (Petzschner & Glasauer, 2011; Petzschner, Glasauer, & Stephan, 2015). The modality- and timescale-dependence of the central tendency observed in the present study suggests that the source of timing noise can be unique to each timescale or each sensory modality, and then, a common computational process realizes the statistical optimality context-dependently for such noisy representation of time.

Study 2:

Context-dependent neural modulations in the
perception of duration

Introduction

As I mentioned in the previous chapter, temporal information in different timescales is related to different behavioral functions, and processed by different neural systems. Previous studies have shown that there are two timing systems divided by a boundary of around one second (Lewis & Miall, 2006). Sub-second timing is involved in motor control (Merchant & Georgopoulos, 2006) and speech generation (Schirmer, 2004), whereas supra-second timing is critical for foraging (Kacelnik & Brunner, 2002) and decision-making (Sohn & Carlson, 2003). Neuroimaging studies have revealed that sub- and supra-second timing differ in terms of their neural implementations (Lewis & Miall, 2003b; Wiener et al., 2010). The processing network for sub-second durations mainly involves the motor system, including the supplementary motor area (SMA), the primary motor area, and the primary somatosensory area, whereas the supra-second network includes the prefrontal cortex, the posterior parietal cortex, and the basal ganglia, which are areas involved in attention and/or working memory (Lewis & Miall, 2006). In physiological studies, duration-tuned neurons have been reported for sub-second timing in such areas as the SMA-preSMA (Crowe, Zarco, Bartolo, & Merchant, 2014; Merchant, Harrington, et al., 2013; Merchant, Perez, Zarco, & Gamez, 2013) and the putamen (Bartolo, Prado, & Merchant, 2014), and for supra-second timing in the prefrontal cortex (Yumoto et al., 2011).

While previous neuroimaging studies have emphasized the distinctions between the sub- and supra-second timing systems (Hayashi et al., 2014; Jahanshahi, Jones, Dirnberger, & Frith, 2006; Lewis & Miall, 2006; Pouthas et al., 2005; Wiener et al., 2010), the nature of continuity between these two systems remains an open question. Psychologically, we can

execute timing tasks whether the target duration is sub-second, supra-second, or around 1 second (i.e., peri-second). Seamless timing across different timescales cannot be realized without some intermediate or transitional state between the sub-second system and the supra-second system. This raises the question: how are peri-second durations processed in our brain? A few studies have indirectly dealt with this issue. A meta-analysis study reported the presence of brain regions that are activated in both sub- and supra-second timing (Wiener et al., 2010). Several fMRI studies have reported that BOLD activities in various brain regions correlate with event durations at timespans ranging from the milliseconds to seconds range (Coull, Charras, Donadieu, Droit-Volet, & Vidal, 2015; Morillon, Kell, & Giraud, 2009; Wencil, Coslett, Aguirre, & Chatterjee, 2010). These fMRI studies, however, assumed a monotonic change of BOLD activity across sub- and supra-second timing, and did not directly investigate the distinction between sub- and supra-second timing. These studies suggest that continuities exist between the sub- and supra-second timing systems. However, no neuroimaging study has directly examined how these two distinct neural timing systems operate for peri-second durations.

One plausible solution for peri-second processing is that both the sub-second and supra-second systems are involved in processing peri-second durations, and therefore, peri-second durations are perceived through cooperation of these two systems. In such a framework, it is predicted that peri-second timing activated both the sub- and supra-second timing systems.

While the transition between timing systems might depend on the duration to be timed, the transition might also depend on the hysteresis of previous trials. It is well known that

stimulus history induces biases in various timing tasks (Jazayeri & Shadlen, 2010; Miyazaki, Yamamoto, Uchida, & Kitazawa, 2006; Shi, Church, et al., 2013). One example of these phenomena is the central tendency in timing, which can be described as follows: when various durations are presented in an intermixed order, relatively shorter durations are overestimated and relatively longer durations are underestimated. This phenomenon occurs across different timescales (Lejeune & Wearden, 2009): When various durations in the milliseconds-to-seconds range are intermixedly presented, shorter sub-second durations are overestimated, and longer durations in the supra-second range are underestimated. These phenomena suggest that duration perception depends on the history of recently presented durations.

Based on these psychophysical observations, which suggest the presence of a hysteresis-based timing mechanism, I hypothesized that peri-second processing relies on the timing system that predominately involves the processing system corresponding to the durations in previous trials. In other words, when peri-second trials are placed in between sub-second trials, the peri-second duration is encoded mainly by the sub-second system. On the other hand, when peri-second trials are placed in between supra-second trials, the peri-second duration is encoded mainly by the supra-second system.

Thus far, I have two independent hypotheses regarding peri-second processing. First, I hypothesized that both the sub- and supra-second timing systems are recruited for peri-second timing. Second, I hypothesized that the durations in previous trials affects peri-second processing. To test these hypotheses, I measured neural activity while subjects performed a duration reproduction task using functional magnetic resonance imaging (fMRI).

Methods

Subjects

Twenty-one healthy volunteers (12 males and 9 females, 18-23 years old) participated in the fMRI experiment. All participants gave written informed consent for their participation in the experimental protocol, which was approved by the institutional review boards of The University of Tokyo. All subjects reported to have normal or corrected-to-normal vision.

Procedure

All visual stimuli were generated using MATLAB with the Psychophysics Toolbox (Brainard, 1997). A schematic of a trial is shown in Figure 2.1. The task was to reproduce the duration of the visually presented Gaussian luminance blob. In the experiment, each trial began with a cue presentation, which informed the subject of the duration to be presented: a single character, S, M, or L, was presented for the sub-, peri-, or supra-second condition, respectively. After a pseudorandom delay (1–2 sec), a green Gaussian blob was presented for a certain duration. The stimulus duration was 0.4 second for the sub-second condition, 1 second for the peri-second condition, or 2.5 seconds for the supra-second condition. Subjects were not explicitly informed that stimulus durations within each condition were constant. After a pseudorandom delay (1–4 sec), the color of the fixation cross changed from white to black (go signal). After viewing this go signal, subjects reproduced the perceived duration of the green stimulus by making a sustained button press that lasted for the perceived duration. All subjects used their left thumb to press the response button.

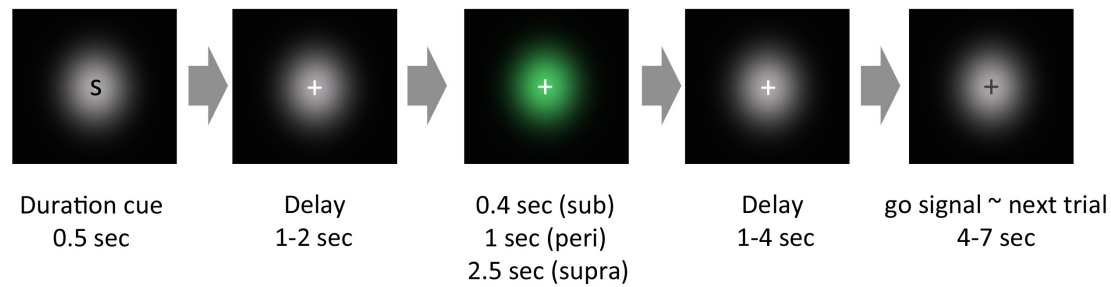


Figure 2.1. Schematic of an experimental trial. In our experimental paradigm, each trial began with a cue presentation, which roughly informed the subjects of the cue duration to be presented. After a pseudorandom delay, a green Gaussian blob was presented for a certain duration. After another pseudorandom delay, the color of the fixation cross changed from white to black. After this change of color, subjects reproduced the perceived duration of the green stimulus by pressing a button.

Subjects completed 10 fMRI runs in total. In half of the runs, the peri-second trials were intermixed with the sub-second trials, and in the other half of the scans, the peri-second trials were intermixed with the supra-second trials. Sub- and peri-second runs contained 20 trials for each duration, resulting in the subjects completing 100 trials in total for each duration within 5 runs. Supra- and peri-second runs contained 16 trials for each duration, resulting in the subjects completing 80 trials in total within the other 5 runs. The runs with sub- and peri-second trials and the runs with supra- and peri-second trials were performed alternately, and the type of run that began each experiment was counterbalanced across subjects. In subsequent contrast analysis, one randomly chosen sub- and peri-second run was discarded to equalize the number of trials used for contrast calculation for all conditions. Therefore, 80 trials for each condition were used in the analysis.

I added a duration cue at the beginning of a trial for the following reason: each run included two distinct durations, and therefore, without the duration cue, subjects could judge whether the stimulus duration was the longer one or the shorter one during stimulus presentation. For example, if no duration cue was presented in the supra-second trials which were intermixed with the peri-second trials, subjects could judge that the presented stimulus duration was the longer one, as it lasted some duration beyond 1 second. By adding the duration cue, which informed the subjects in advance of the duration to be presented, I aimed to prevent the possibility that the brain activity induced by categorical judgment about the stimulus duration would contaminate timing-induced brain activity during stimulus presentation.

MRI Data Acquisition

MRI data was acquired using a 3T MRI system (Magnetom Prisma, Siemens, Erlangen, Germany), equipped with a 64-channel head coil. For each subject, a high-resolution anatomical scan (MPRAGE) was performed. The total data acquisition time for the anatomical scan was 4.7 min (TR = 2 s, TE = 2.9 ms, flip angle = 9 deg, matrix size = $240 \times 256 \times 176$, spatial resolution = $1 \times 1 \times 1 \text{ mm}^3$). EPI sequences (TR = 2 s, TE = 30 ms, flip angle = 90 deg) were used to obtain functional MR images. Thirty-nine contiguous slices ($3 \times 3 \times 3.5 \text{ mm}^3$, with 10% gap) oriented parallel to the AC-PC plane were acquired to cover the whole brain, using an interleaved slice acquisition sequence. The total time for each functional run was 6.2 min.

Data Analysis

FS-FAST and FreeSurfer (<http://surfer.nmr.mgh.harvard.edu>) software were used for the data analysis. For image preprocessing, all functional images were head motion corrected, slice-time corrected, spatially smoothed with a Gaussian kernel of 8.0 mm (FWHM). The mean

intensity for the entire functional volume was computed for each scan. The global mean of the entire brain was rescaled so that the same mean was set across scans. All functional data were registered to the individual anatomically reconstructed brain.

Hemodynamic responses evoked by different task components were modeled as single events convolved with a canonical hemodynamic response function. Events time-locked to the presentation of the stimuli and the onset time of reproduction were defined separately for each duration condition, that is, sub-second, peri-second intermixed with sub-second, peri-second intermixed with supra-second, and supra-second durations. This resulted in eight distinct event types: 2 task components (stimulus/reproduction) \times 4 durations. Duration of the stimulus event was defined as duration of the stimulus presentation, and duration of the reproduction event was defined as the reproduced duration. In the present study, I used a rapid event-related design. In the experiment, events were closely spaced, resulting in substantially overlapped hemodynamic responses. However, previous studies have shown that the underlying hemodynamic responses can be computationally deconvolved by randomly jittering inter-event intervals and under the assumption of linearity (Burock, Buckner, Woldorff, Rosen, & Dale, 1998; Dale & Buckner, 1997). Using relatively long and varying intervals between the stimulus interval and the reproduction interval allowed temporal deconvolution of the BOLD response for the stimulus interval and the reproduction interval (Coull, Nazarian, & Vidal, 2008). To examine brain activity manifest by duration encoding, events in the stimulus phase were used for the following contrast analysis. I eliminated activation elicited by duration reproduction from the contrast analysis, because any change of BOLD response depending on duration condition can be attributable to the effect of the variation of reproduced durations in each

duration condition, or memory decay derived from the variation of time from trial onset.

In the analysis, I first identified brain regions related to sub- and supra-second timing by contrasting the BOLD response for the sub-second stimulus presentation and that for the supra-second stimulus presentation. Then, to identify regions involved in peri-second timing, I compared the BOLD response for the peri-second stimulus presentation to either the BOLD response for the sub- or the supra-second stimulus presentation. In the experiment, the sub- and supra-second trials appeared in half of the total of 10 runs, while the peri-second trials appeared in all runs. To compensate for the number of trials needed to calculate the BOLD contrast, I compared the BOLD responses between the trials presented in the same type of runs: the BOLD responses for the sub-second stimulus were contrasted to that for the peri-second stimulus intermixed with the sub-second trials, while the BOLD response for the supra-second stimulus were contrasted to that for the peri-second stimulus intermixed with the supra-second trials. Finally, to examine the hysteresis of the previous trials, the BOLD response for the peri-second stimulus intermixed with the sub-second trials was compared to the BOLD response for the peri-second stimulus intermixed with the supra-second trials. These two types of peri-second conditions had the same stimulus and same duration, and were different in terms of intermixed trials that were either sub- or supra-second trials.

One of the difficulties in neuroimaging studies of time perception is the use of control tasks. Some studies have compared brain activity of subjects while they were executing a timing task with that of subjects executing a control task (e.g., color task) in response to the same stimuli (Coull, Vidal, Nazarian, & Macar, 2004; Morillon et al., 2009). These studies defined the regions that exhibited greater activities in the timing task as “timing-related” regions.

However, Livesey et al. (2007) reported that some of these “timing-related” activities are attributable to differences in the difficulties of the timing versus control tasks (Livesey, Wall, & Smith, 2007). To eliminate the effect of task difficulty in the control task in the present study, I did not employ any explicit control tasks. Alternatively, I directly compared brain activities when subjects were timing the presented stimulus. Given that the stimuli used in all conditions were the same Gaussian luminance blobs and the task was always to reproduce the presented duration, the only thing that was different across conditions was the stimulus duration.

Results

Behavioral Data

The mean and SD of the reproduced duration was 657.0 ± 166.6 ms for the sub-second trials, 1223.8 ± 215.4 ms for the peri-second trials intermixed with the sub-second trials, 1348.0 ± 265.4 ms for the peri-second trials intermixed with the supra-second trials, and 2358.1 ± 289.7 ms for the supra-second trials.

To test the contextual effect of previous trials, I first conducted a two-way repeated-measures ANOVA with run type (sub- and peri-second run or peri- and supra-second run) and relative duration within a run (short or long) as factors. To compensate the difference of stimulus durations across conditions, the ratio of the reproduced duration to the stimulus duration was tested as an index of duration estimation error. If the central tendency occurs, the relatively short duration within a run should be overestimated, and the relatively long duration within a run should be underestimated. That is exactly what I found.

As shown in Figure 2.2, there were a significant main effect of relative duration

within a run ($F(1,80) = 46.84, p < .001$) and of run type ($F(1,80) = 22.84, p < .001$). No significant interactions were found ($F(1,80) = 0.01, p = .91$). These results indicate that the central tendency occurred in both run types, and that durations were more overestimated in runs with sub- and peri-second trials than in runs with supra- and peri-second trials.

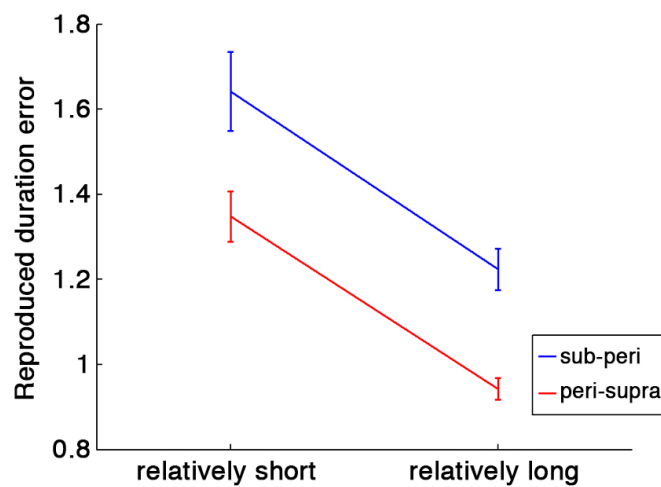


Figure 2.2. Duration estimation errors calculated as ratios of the reproduced duration to the stimulus duration. Blue line indicates the duration estimation errors in runs with sub- and peri-second trials, and red line indicates the duration estimation errors in runs with peri- and supra-second trials. Error bars indicate standard errors (SE). Horizontal axis represents relative duration within each run: in runs with peri- and supra-second trials, for example, the peri-second durations are the relatively shorter durations and the supra-second durations are the relatively longer durations.

Furthermore, I tested the contextual effect in peri-second timing. The reproduced

duration for the peri-second trials intermixed with the supra-second trials was significantly longer than those for the peri-second trials intermixed with the sub-second trials ($t(20) = 4.72$, $p < .0001$, $d = 1.03$). This tendency was highly consistent across individuals (19 out of 21 subjects exhibited this tendency). This result indicates that the duration of previous trials affected the perceived duration of the peri-second stimulus. It should be noted that the reproduced durations for peri-second trials were longer than 1 second both for the peri-second trials intermixed with the sub-second trials ($t(20) = 4.76$, $p = .0001$, $d = 1.04$) and for the peri-second trials intermixed with the supra-second trials ($t(20) = 6.01$, $p < .0001$, $d = 1.31$). The overestimation in reproduced duration for sub- to peri-second durations is consistent with a previous study (Shi, Ganzenmüller, & Müller, 2013).

fMRI Data

I first determined brain regions that exhibited different activation patterns between the sub- and the supra-second timing. When the subjects timed sub-second stimuli, the bilateral SMA, the bilateral visual cortex, the left premotor area, the right intra-parietal sulcus (IPS), and the right precentral and postcentral region were activated. By contrast, when subjects timed supra-second stimuli, significant activations in the inferior frontal gyrus (IFG), the superior frontal gyrus (SFG), the superior parietal cortex, the superior temporal cortex, the lingual gyrus, the putamen, and the ventral cerebellum were observed (Figure 2.3, Table 2.1). The timing networks I described are largely consistent with previously reported sub- and supra-second timing networks (Lewis & Miall, 2003b; Wiener et al., 2010) and confirm that sub-second timing versus supra-second timing depend on distinct brain networks. However, it should be noted that I observed the activation of the cerebellum in supra-second timing, whereas the

cerebellum is often reported to be involved in the sub-second timing network (Lewis & Miall, 2006; Wiener et al., 2010).

Secondly, to determine the brain regions activated when subjects were timing the peri-second duration, I calculated the contrast between peri- and supra-second timing, and the contrast between peri- and sub-second timing (Figure 2.3, Table 2.1). In comparison with sub-second timing, peri-second timing activated the superior parietal cortex, the superior temporal cortex, the lingual gyrus, and the ventral cerebellum. These areas were mostly activated in supra-second timing, and were therefore included in the supra-second system. In contrast, when compared to supra-second timing, peri-second timing activated the SMA, the precentral area, the supramarginal gyrus, and the visual cortex. These areas were mostly activated in sub-second timing, and therefore included the sub-second system. As described above, peri-second timing thus activated both the sub- and the supra-second timing networks. These results suggest that duration at the boundary between the sub- and the supra-second is processed by a combination of the sub- and the supra-second systems.

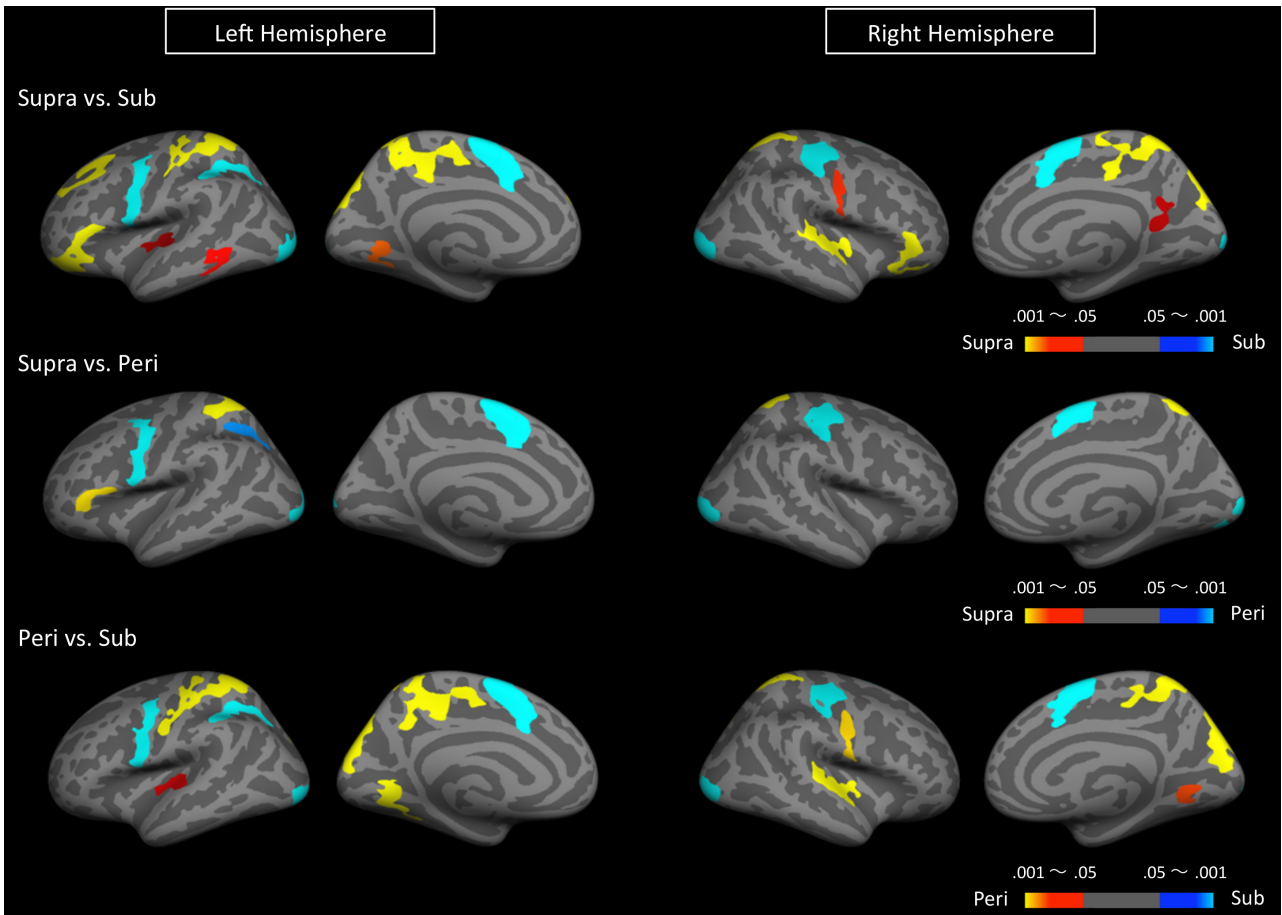


Figure 2.3. Significantly activated clusters in sub-, peri-, and supra-second timing. The color scales indicate the cluster-wise corrected P-values.

Table 2.1. Brain regions significantly activated by either sub-, peri-, or supra-second timing. MNI coordinates of peak activation and cluster-wise corrected P-values are presented for each cluster.

Anatomical description	si de	MNI coordinates				MNI coordinates				MNI coordinates			
		X	Y	Z	P-value	X	Y	Z	P-value	X	Y	Z	P-value
		Supra>Sub				Supra>Peri				Peri>Sub			
Frontal													
Superior frontal gyrus	L	-22	22	49	0.0001								
Inferior frontal gyrus	L	-34	45	-11	0.0001	-51	32	4	0.0013				
	R	51	33	-5	0.0001								
Precentral	R	43	-10	37	0.0086								
Parietal													
Paracentral	L	-10	-17	48	0.0001					-10	-17	48	0.032
Postcentral	R									63	-8	12	0.025
Superior parietal cortex	L	-18	-86	37	0.0001	-31	-46	56	0.0001	-18	-86	37	0.0001
	R	22	-82	41	0.0001	22	-51	60	0.0002	21	-83	41	0.0001
Precuneus	R	15	-46	56	0.0001					12	-47	65	0.0001
	R	10	-54	11	0.027								
Temporal													
Superior temporal cortex	L	-44	-23	3	0.039					-53	-19	4	0.034
	R	38	-13	4	0.0001					54	-24	6	0.0001
Middle temporal cortex	L	-60	-52	-3	0.013								
Occipital													
Lingual	L	-15	-61	0	0.005					-14	-61	0	0.0001
	R									8	-63	5	0.0068
Subcortical													
Cerebellum	L	-28	-41	-47	0.0001	-37	-47	-30	0.0001	-30	-43	-47	0.0001
	R	18	-55	-55	0.0016					20	-51	-57	0.0026
Putamen	R	22	1	-8	0.0158								
		Sub>Supra				Peri>Supra				Sub > Peri			
Frontal													
Pre-SMA/SMA	L	-11	11	43	0.0001	-6	0	64	0.0001	-7	-2	64	0.0001
	R	7	3	66	0.0001	8	1	57	0.0007	8	3	66	0.0001
Precentral	L	-58	6	27	0.0001	-53	-4	44	0.0001	-57	6	27	0.0001
	R	37	-19	57	0.0001	37	-20	59	0.0001	37	-19	57	0.0001
Parietal													
Supramarginal gyrus	L	-41	-43	39	0.0001					-44	-45	40	0.0001
Superior parietal cortex	L					-27	-61	45	0.003				
Occipital													
Visual cortex	L	-26	-96	-8	0.0001	-26	-96	-8	0.0001	-27	-96	-8	0.0001
	R	28	-97	-5	0.0001	27	-98	-5	0.0001	24	-99	-8	0.0001

Finally, to examine the effect of recent trials on peri-second processing, I compared brain activity for peri-second timing intermixed with sub-second timing with brain activity for peri-second timing intermixed with supra-second timing (Figure 2.4, Table 2.2). The right precentral and postcentral areas were more activated in peri-second trials intermixed with sub-second trials. These areas were also activated in sub-second timing, and are thus thought to be included in the sub-second system. In contrast, the right IPL was more activated for the peri-second trials intermixed with supra-second trials. The right IPL did not exhibit differential activity between sub- and supra-second timing in the present study, hence, there is no simple interpretation of the contextual effect in the right IPL. The right IPL has been linked to supra-second timing in previous studies (Lewis & Miall, 2002; Macar et al., 2002), therefore, I speculate that the right IPL activation in peri-second trials intermixed with supra-second trials might reflect the involvement of the supra-second timing system. These results suggest that the timing network which was activated by the recently presented durations predominates in peri-second timing. More specifically, when the subject frequently times sub-second durations, the peri-second duration is processed with a larger contribution from the sub-second system; when the subject frequently times supra-second durations, the peri-second duration is processed with a larger contribution from areas that have previously been associated with supra-second timing.

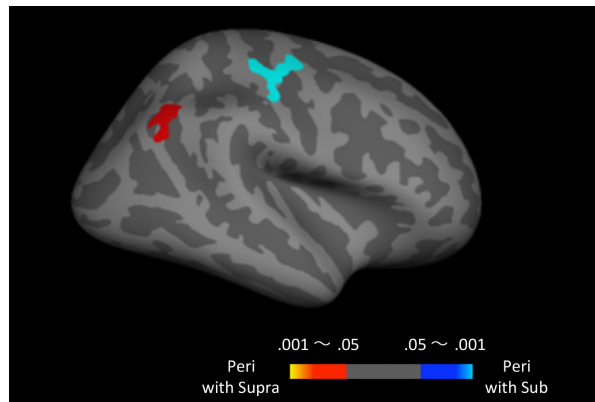


Figure 2.4. Peri-second trials intermixed with supra-second trials versus peri-second trials intermixed with sub-second trials. The color scales indicate the cluster-wise corrected P-value.

Table 2.2. Brain regions that exhibited context-dependent time processing.

BOLD contrasts were calculated between peri-second trials intermixed with supra-second trials and peri-second trials intermixed with sub-second trials. MNI coordinates of peak activation and cluster-wise corrected P-values are presented for each cluster.

Anatomical description	side	MNI coordinates			P-value
		X	Y	Z	
Peri with Supra > Peri with Sub					
Inferior parietal lobule	R	48	-60	41	0.0222
Peri with Sub > Peri with Supra					
Precentral	R	38	-12	63	0.0001

Discussion

In the present study, I examined the neural correlates of duration perception in the milliseconds-to-seconds time range using fMRI. The present results indicated that: 1) distinct brain networks are involved in sub- versus supra-second timing (in accordance with previous studies), 2) both the sub- and supra-second timing networks work in cooperation in encoding peri-second durations, and 3) the processing mechanism for peri-second durations is context dependent in that peri-second timing relies more on the timing system that processed durations presented in recent trials.

Distinctions between the sub-second system and the supra-second system

By comparing brain activities during sub-second timing and those during supra-second timing, I confirmed the presence of two separate timing systems for these two time ranges, as previous studies have reported (Hayashi et al., 2014; Jahanshahi et al., 2006; Lewis & Miall, 2003b; Pouthas et al., 2005; Wiener et al., 2010). Moreover, the activity patterns observed for sub- and supra-second timing in the present study were largely consistent with previous studies. Frontal and posterior parietal areas of the cortex, which are related to working memory or attention, were involved in supra-second timing, while motor and somatosensory systems, including the SMA, postcentral, and precentral areas, were activated in sub-second timing.

One exception might be my observation of activation in the cerebellum during supra-second timing. While several studies have reported that the cerebellum engages in sub-second timing (Lewis & Miall, 2006; Wiener et al., 2010), a meta-analysis by Lewis and

Miall (2003b) reported that the cerebellum also contributes to supra-second timing. Thus, the role of the cerebellum in duration perception is still under debate. Harrington et al. (2004) showed that patients with cerebellar damage exhibited greater timing-related variability in a time reproduction task, but not in a time-perception task, and that this timing-related variability correlated with working memory performance (Harrington, Lee, Boyd, Rapcsak, & Knight, 2004). They concluded that the cerebellum might process task-relevant cognitive information when it involves the motor-output system. The observation of cerebellar activation in supra-second timing in the present study is consistent with their findings. Further study will be needed regarding the role of the cerebellum in timing perception in the milliseconds-to-seconds range.

Transitional state in peri-second processing

In the present study, the peri-second duration preferentially activated the sub-second system versus the supra-second system, or vice-versa, depending on context. These results suggest that temporal processing for the peri-second duration relies on a transitional state, in which both the sub- and supra-second timing systems work in cooperation.

Behavioral results showed that the reproduced durations for both peri-second conditions were greater than one second. The overestimation of peri-second durations in the reproduction task is also reported by a previous study (Shi, Ganzenmüller, et al., 2013). The over-reproduction and the simultaneous activation of the sub- and supra-second system in peri-second timing might raise a question regarding the fluctuation of the categorical boundary between the sub- and supra-second systems. The durations used in the present study were selected based on the assumption that the boundary between the sub- and supra-second timing

systems lies at around one second (Lewis & Miall, 2006). In actuality, there exist controversies over the precise boundary between the two systems. A psychological meta-analysis study reported that the boundary lies at around 1500 ms (Gibbon et al., 1997), other researchers suggested that the boundary lies at around 500 ms (Rammsayer, 1999; Rammsayer & Lima, 1991). In the present study, I showed that both the sub- and supra-second systems are recruited for peri-second timing. If a boundary lies either at 1500 ms or 500 ms, and two timing systems distinctly switch their operation by this precise boundary, the simultaneous activation of the sub- and supra-second timing systems would not be observed at one second. The present results can be explained if I assume the boundary exists precisely at around one second, however, this assumption is not very congruent with previous psychological studies. Rather, these results imply another possibility that the durations that the sub- and supra-second timing systems can process widely overlap at around one second. Previous psychological and neuroimaging studies have reported that different timing system is recruited depending on the task and stimulus modalities (Lewis & Miall, 2003b; Merchant, Harrington, et al., 2013; Merchant et al., 2008; Wiener et al., 2010). The categorical boundary between the sub- and supra-second durations might fluctuate within relatively widely overlapped durations between the sub- and supra-second timing systems, depending on the stimulus and task features. Because I tested only one-second duration in the present study, I cannot dissociate whether two timing systems have a precise boundary or widely overlap around 1 second. Further study will be needed to examine the transition from the sub-second system to the supra-second system.

Many studies, including the present study, have compared neural correlates of sub- and supra-second timing by using distinctly different durations (Jahanshahi et al., 2006; Lewis

& Miall, 2003a; Pouthas et al., 2005). In these cases, subjects were able to make a categorical judgment regarding whether the presented stimulus duration is relatively shorter or longer within an experimental session. Therefore, one might argue that the sub-second and supra-second systems do not code the absolute duration, but rather the relative duration within an experimental session. That is, the so-called “sub-second” system might process relatively shorter durations, while the so-called “supra-second” system might process relatively longer durations within a session. If this is indeed the case, it implies that the activation of the sub- and the supra-second systems in peri-second timing might not represent a transitional state between the sub- and supra-second systems.

If the “sub-second” system and the “supra-second” system respectively code “relatively shorter” and “relatively longer” durations, the peri-second trials intermixed with the sub-second trials would activate the supra-second system, because the peri-second trials had a relatively longer duration in runs with sub- and peri-second trials. Similarly, the peri-second trials intermixed with the supra-second trials would activate the sub-second system, because peri-second trials are relatively shorter in duration in runs with the supra- and the peri-second trials. However, the present results contradicted these predictions, and therefore, relative duration coding by the sub- and supra-second systems is unlikely. It is certainly a possibility that the difference between the two peri-second conditions was not optimized to detect brain activity coding relative durations. However, in addition to the present results, previous studies have suggested that the sub- and supra-second systems code absolute durations: Distinct activation in the sub- and supra-second systems has been reported even when multiple durations are not used in the task, and therefore, no information regarding relative duration was included

in this task (Lewis & Miall, 2003a; Wiener et al., 2010). Thus, on the whole, it is unlikely that the sub- and supra-second system code relative duration information. Therefore, activation of both the sub- and supra-second systems in peri-second timing suggests that the peri-second duration perception system is a transitional state between the sub- and supra-second systems.

Such a transitional timing mechanism between different timescales might enable a seamless representation of time. Many psychological and neuroimaging studies have investigated the distinctions between the sub-second and supra-second systems using temporal tasks with various durations spanning different timescales (Gibbon et al., 1997; Hayashi et al., 2014; Koch, Oliveri, & Caltagirone, 2009; Lewis & Miall, 2003a, 2009; Rammsayer, 1999). These studies found there were differential brain activities or behavioral measures between sub- and supra-second timing, indicating that distinct psychological or neural mechanisms are recruited for sub- and supra-second timing. An oversight of these studies was that subjects executed the same timing tasks for durations of different timescales. The fact that the human observers can execute timing tasks whether the target duration is sub-second or supra-second suggests the presence of continuous or common mechanisms across the sub-second system and the supra-second system. Based on confirmatory factor analysis, Rammsayer & Troche (2014) proposed a hierarchical mechanism of duration perception in which an timescale-independent superordinate processing system controls the sub- and supra-second timing mechanisms (Rammsayer & Troche, 2014). This superordinate common mechanism is certainly a possible means to realize seamless duration perception across different timescales. However, the transitional processing mechanism in the peri-second duration suggested by the present study represents another possibility. Even if no superordinate system exists, the continuity of the

sub-second system and the supra-second system in the peri-second range might enable the execution of timing tasks across different timescales. It should be noted that these two possibilities are not mutually exclusive, and further research is necessary to determine how these common or continuous mechanisms interact with each other.

Context-dependent modulations of peri-second processing

The present results indicate that the processing mechanism used to perceive peri-second durations changes context-dependently; that is to say, peri-second timing relies more on the timing system which processed durations presented in recent trials. I also observed this contextual effect in the behavioral results. The reproduced duration for the peri-second trials was longer when they were intermixed with the supra-second trials, compared to when they were intermixed with the sub-second trials.

While peri-second timing intermixed with sub-second timing activated the right precentral area that was also activated during sub-second timing, peri-second timing intermixed with supra-second timing activated the right IPL that was not activated during supra-second timing. Hence, there is no simple interpretation of the contextual effect in the right IPL. Previous studies have reported activation in the right IPL during supra-second time reproduction tasks (Lewis & Miall, 2002; Macar et al., 2002). Moreover, the IPL has anatomical connections with the inferior frontal cortex and the auditory cortex (Caspers et al., 2011; Caspers et al., 2013), which were activated in supra-second timing in the present study. Therefore, I speculate that the right IPL activation in peri-second timing intermixed with supra-second timing might reflect the involvement of the supra-second timing system.

In the present study, context-dependent encoding of time was observed only in the

right hemisphere. It is known that various timing tasks activate predominantly right-sided networks (Battelli, Pascual-Leone, & Cavanagh, 2007; Coull, Davranche, Nazarian, & Vidal, 2013; Rao, Mayer, & Harrington, 2001). In particular, the right posterior parietal lobe, where greater activation was found in peri-second trials intermixed with supra-second trials, has been proposed to be a core region for timing (for a review, Battelli et al, 2007). Regions surrounding the central sulcus correspond to the primary motor and primary somatosensory areas, where greater activation was found in peri-second trials intermixed with sub-second trials, have also been reported to engage in the sub-second timing (Lewis & Miall, 2003b). It should be noted that all the contrasts found in the present analysis were computed with regressors time-locked to the stimulus presentation. Therefore, precentral (primary motor area) and postcentral (primary somatosensory area) activation in the peri-second duration intermixed with the sub-second duration would not reflect differences in reproduced durations between two peri-second conditions.

Even though contrasting activation patterns were computed by regressors for the stimulus presentation phase, the difference in brain activity between two peri-second conditions corresponded to the reproduced duration. The peri-second trials intermixed with sub-second trials activated the precentral area, which is a part of the sub-second system observed in the present study, and the reproduced duration of these trials was shorter than the reproduced duration of the peri-second trials intermixed with supra-second trials, which activated the right IPL, which has been linked to supra-second timing in previous studies. Almost all of the previous neuroimaging studies examining neural correlates of perceptual duration used illusions of time, in which looming, moving, or flickering visual stimuli appeared to be longer than static

stimuli (Buetti & Macaluso, 2011; S. K. Herbst, Chaumon, Penney, & Busch, 2014; Sophie K. Herbst, Javadi, van der Meer, & Busch, 2013; Wittmann, van Wassenhove, Craig, & Paulus, 2010). Because these studies manipulated the perceptual duration by changing stimulus features, whether the detected brain activities were related to changes in perceptual duration or stimulus features was not dissociable. In contrast, in the present study, differential brain activity that depended on the hysteresis of durations in previous trials was detected between physically identical visual stimuli. Therefore, the brain activity detected between two peri-second conditions can be attributed to context-dependent timing processing and the corresponding change of the perceptual duration.

Studies with Bayesian modeling have revealed that the temporal variability of perceived duration induces the contextual effect such as the central tendency (Jazayeri & Shadlen, 2010; Petzschner et al., 2015; Shi, Church, et al., 2013). For the time reproduction task, when a single duration is presented and then subjects reproduce its duration, the temporal variability of the reproduced duration is larger compared to when multiple durations are presented (Grondin, 2012, 2014). The contextual effect of the reproduced duration observed in the present study might reflect the inherent large temporal variability of the single duration reproduction task and Bayesian inference process. The context-dependent modulations of timing systems suggest that the brain optimally encodes stimulus duration based on the history of previous trials, as many psychophysical and modeling studies have suggested (Cicchini et al., 2012; Jazayeri & Shadlen, 2010; Lejeune & Wearden, 2009; Petzschner et al., 2015; Shi, Church, et al., 2013). The present study thus found the neural correlate of these proposed context-dependent timing systems. These systems would help to efficiently encode duration

under noisy conditions and in different temporal contexts, and might be responsible for Bayesian process in duration perception.

Previous studies have shown that the timing system that is used depends not only on stimulus duration, but also on various stimulus features and/or task dimension. Whether or not the duration is defined by movement, whether a stimulus is continuous or not (Lewis & Miall, 2006), and possibly stimulus modality (Yuasa & Yotsumoto, 2015) can all modulate the selection of the timing network. In addition to these stimulus or task features, the hysteresis of previous trials is also a factor for encoding stimulus duration optimally.

General Discussion

In this doctoral thesis, I have revealed the psychological and neural mechanisms that realize the optimal encoding of event duration. Detailed discussions being included in each preceding chapter, here, I dwell on the novelties and implications of my studies.

Previous studies have sporadically reported the properties of the central tendency by using a specific sensory modality or timescale. In Study 1, I investigated the central tendency in a comprehensive manner across sensory modalities and timescales, and revealed the modality-dependent nature in the sub-second range and the modality-independent nature in the supra-second range. In addition, I argued that some assumptions in previous computational modeling studies, the scalar property and the disregard of the modality effect for instance, can be sometimes violated. The present psychophysical study will prompt a rethink of previous Bayesian models of duration perception.

In Study 2, by using fMRI, I demonstrated that the sub- and supra-second timing networks in the brain are not completely separable, but they cooperatively encode peri-second durations. Furthermore, I found that the timing system which processes durations presented in previous trials is more involved in subsequent peri-second processing. This study will shed light on the neural implementation of the optimal encoding process of event duration.

Temporal context effect such as the central tendency shows the past experience shapes the perception of the present. In the central tendency, the duration perception in the present is biased *toward* durations presented in the past. In contrast to such an assimilative context effect, a contrastive temporal context effect has also been reported: The perception of duration is sometimes biased *away from* durations presented in the past (Heron et al., 2012; Walker, Irion, & Gordon, 1981). In this so-called duration adaptation effect, after repeated

exposure to relatively longer durations, a subsequent intermediate duration is perceived shorter; after repeated exposure to relatively shorter durations, the subsequent intermediate duration is perceived longer. A notable difference in task requirement between the central tendency and the duration adaptation is the presence of judgments for previously presented durations. When subjects have to make judgments about every sequentially presented duration, the central tendency is observed. In contrast, the duration adaptation occurs when subjects just passively observe the adapting durations and make judgments only about the subsequently presented duration. These two phenomena are also different in terms of computational account. While the central tendency can be accounted for in the framework of Bayesian inference (Figure 4.1 a), the channel-based model is a predominant computational model for the duration adaptation (Figure 4.1 b). The channel-based model assumes that the duration of a stimulus is coded by a population of channels that are tuned to various durations. Adaptation to a specific duration selectively suppresses the activity of channels that are tuned around the adapted duration. Then, a subsequently presented stimulus at another duration elicits the channels' activity, but the responses of the adapted channels are weakened. This distortion in the activity-distributions across channels generates the aftereffect induced by adaptation (Heron et al., 2012; Murai, Whitaker, & Yotsumoto, 2016). By using an fMRI adaptation technique, a recent neuroimaging study demonstrated that the supramarginal gyrus, the anterior part of the inferior parietal lobule (IPL), exhibits such a duration-tuned neural activity (Hayashi et al., 2015). In Study 2, on the other hand, I revealed the context-dependent neural encoding of duration, which is consistent with the central tendency, in the posterior part of the IPL (Figure 4.1 c). These two studies unveiled that the IPL plays an important role in duration encoding based on the temporal

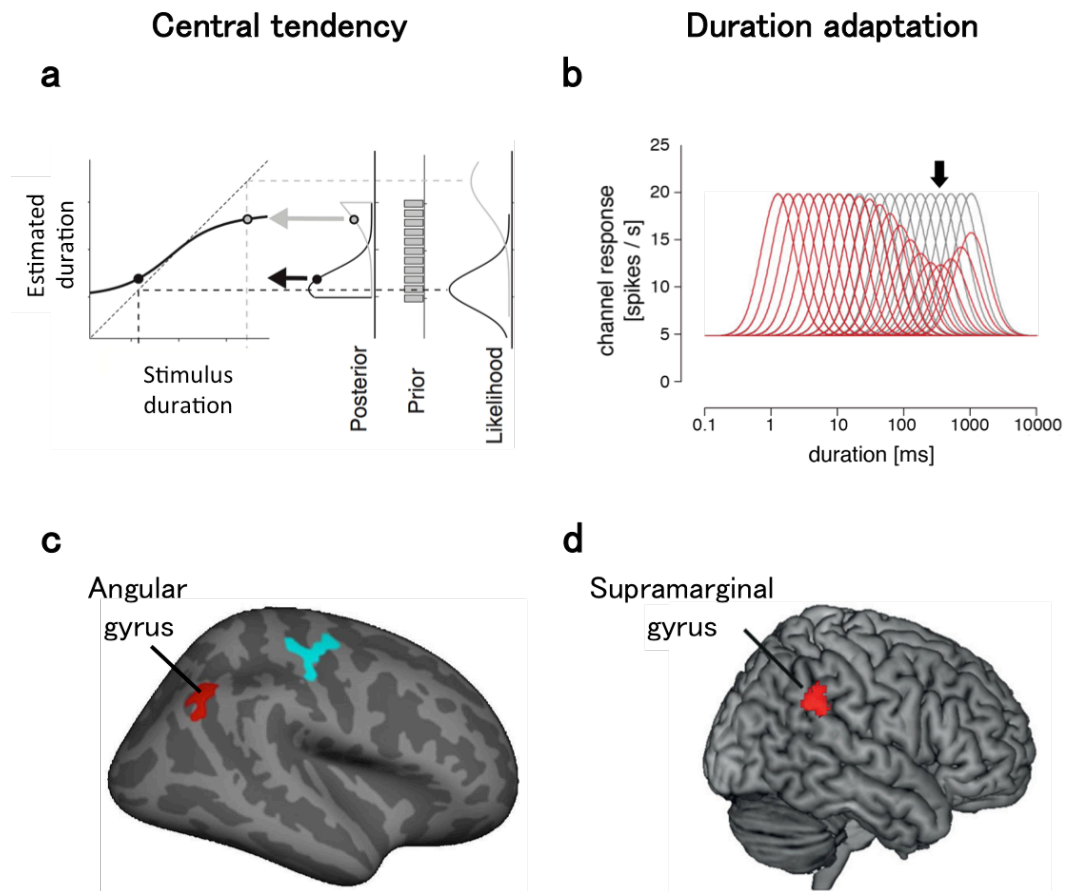


Figure 4.1 The computational models and neural bases of the central tendency and the duration adaptation. (a) A Bayesian model of the central tendency, adapted from Jazayeri & Shadlen (2010). Both the noisy representation of a stimulus duration (likelihood) and the prior knowledge about the distribution of stimulus durations determine a posterior distribution of the perceived duration, based on which subjects make their decisions. (b) The channel-based model of the duration adaptation. Each Gaussian distribution depicts the tuning curve of each duration channel. Normal responses of the duration channels are presented as gray lines. After adaptation to a specific duration (arrow), channel responses around the adapting duration are weakened (red lines), thereby distorting the group response to a subsequent test duration. (c) The context-dependent neural encoding of duration in the angular gyrus (Study 2). (d) The duration-tuned neural activity in the supramarginal gyrus, reported by Hayashi et al. (2015).

context, and that the anterior and posterior subregions of the IPL are distinctively related to the contrastive and assimilative context effect, respectively.

In the present doctoral thesis, I focused on the central tendency of event durations. The central tendency has been widely reported for various perceptual attributes including duration (Cicchini et al., 2012; Jazayeri & Shadlen, 2010), depth, angle (Petzschner & Glasauer, 2011; Petzschner et al., 2015), and stimulus length (Laming, 1999). Some researchers have proposed that duration shares the processing mechanism with other perceptual attributes such as size and numerosity, and that these attributes represent the spatial and temporal “magnitude” of external events (Walsh, 2003). The cortical areas that are commonly activated by the processing of duration, size and numerosity include the posterior parietal area and the prefrontal area (Buetti & Walsh, 2009; Hayashi et al., 2013; Walsh, 2003), which correspond to the supra-second timing network reported in previous studies (Lewis & Miall, 2003a, 2006; Wiener et al., 2010) and also in Study 2 of the present doctoral thesis. Study 1 demonstrated that the central tendency in the supra-second range is modality-independent, and the central tendency in the supra-second range could be interpreted in a more general computational process beyond duration perception. If a common “magnitude” system governs the central tendency of the magnitude metrics, the central tendency in duration perception could be correlated with the central tendency in other perceptual attributes. My studies brought about understandings as to psychological and neural mechanisms of context-dependent duration encoding, and will have expandability to a broader optimization process of our perception.

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