論文の内容の要旨

論文題目　**The Encoding and Maintenance of Time Intervals in Visual Working Memory and the Underlying Neural Mechanisms**

（視覚の作業記憶における間隔時間の符号化と維持およびその神経機序の検証）

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Time is a dimension of experience of events, as well as the content in the experience. How does this so-called time dimension of the mind become the temporal content in the mind? In other words, how the perceived time is stored in the memory? Psychological time consists of three major aspects, such as temporal order, temporal perspective, and time interval/duration. This thesis focuses on the perception of the time interval/duration. Interval timing perception is referred to as the perception of time intervals from hundreds of milliseconds to hundreds of seconds. This range of time intervals is important for many conscious behaviors, and various models have been proposed to explain the cognitive and neural mechanisms underlying the interval timing perception. Additionally, various kinds of perception, including interval timing perception, are known to involve working memory, which is the online workspace for actively maintaining and manipulating information to be used by the ongoing tasks. In a very recent integrative model, interval timing perception and working memory of time intervals are considered to share the same processes and neural mechanisms.

Traditionally, studies for the interval perception have mainly focused on a single time interval, and models for interval perception have been proposed based on the perception of a single time interval.

Therefore, how multiple time intervals are perceived and represented in working memory has been much less studied. Besides, as no studies have directly compared working memory for time intervals with that for other modalities such as visual textures, it is not clear whether the working memory representations for time intervals are comparable to those for other modalities.

Working memory for visual textures consists of encoding, maintenance, and retrieval/decision stages of processing. Therefore, if working memory for time intervals has similar characteristics, we should be able to assume the same stages of processing. Noisy exemplar model, a widely-accepted model for representations of visual memory, assumed each visual texture is stored discretely as a noisy exemplar, and explained characteristics for human visual texture memory using similarities between the exemplars. While noisy exemplar model for visual texture memory has been well studied with various visual items, whether time intervals of visual events can be represented in the same way remains unknown. Therefore, in Study1, I investigated how time intervals are represented in working memory, using Sternberg's recognition task. I compared the typical characteristics of working memory for time intervals with those for visual textures, with regards to the effects of memory load, serial position, and similarity, and investigated these characteristics in the framework of signal detection theory, for sub-second intervals and supra-second intervals. Participants judged whether the probe item matched one of the study items, in either the temporal dimension or in the visual dimension. Results showed similar characteristics of working memory for time intervals and for visual textures. Yet, there was still a difference between time interval memory and visual texture memory. Specifically, the recency effect for time intervals was smaller or even absent, as compared to that for visual textures. Further, as compared with visual textures, sub-second intervals were more likely to be judged as remembered in working memory. Results demonstrated that time intervals can be represented in working memory as discrete items, similarly to visual objects.

Confirming that the time intervals are stored as discrete items in the working memory, in Study 2, I investigated how the time intervals are encoded in the working memory. Two major classes of models have been proposed to explain the encoding of the time intervals. One is an intrinsic model, which propose that timing is embedded in and derived from the neural dynamics, assuming there is no specialized system for processing temporal information. The other is a dedicated model, which assumes some sort of specialized mechanism to function as a clock, to measure time. Among them, the most feasible and developed dedicated model is the Striatal Beat-Frequency (SBF) model. The SBF model proposes that the cortical neurons serve as oscillators of which the oscillating activity contains temporal information, and the medium spiny neurons in the striatum act as detectors. The measured time depends on the detectors detecting the coincident activation patterns of the oscillators, thus modulations of neural oscillations would affect working memory of time intervals. In the SBF model, periodic events like visual flickers are considered to induce the overestimation of time intervals of the events, by driving the neural oscillations to synchronize to the external driving frequency. Such modulation to the neural oscillations by the external stimulations is called neural entrainment. Visual flicker is not the only external stimulation that induces neural entrainment. Transcranial Alternating Current Stimulation (tACS), an electrical brain stimulation with sinusoidal currents applied to the scalp, can directly entrain neural oscillations, and thus can help investigate the causal relationships between neural oscillations and the cognitive functions. In Study 2, I employed the time reproduction task to examine how periodic events modulate the encoding of time intervals. Especially, I examined how visual flickers and tACS affect the encoded time intervals. In the analyses, I analyzed the reproduced durations and the coefficient of variations, which could be used an indicator of the scalar property of interval timing perception. Larger coefficient of variations indicate noisier representations, and smaller coefficient of variations indicate less-noisier representations. In the experiments, the participants remembered the standard interval and then reproduced it after some delay. The standard intervals were defined by flickering visual stimulus or static visual stimulus. tACS was applied during the standard intervals. Results showed the typical flicker-induced time dilation: the reproduced duration was longer with the flickering stimuli. tACS also induced a weak time dilation: the reproduced duration was longer with tACS. Most importantly, both visual flickers and tACS reduced the coefficient of variations, indicating both visual flickers and tACS reduced noise in the represented time intervals. These results demonstrated that periodic stimulations lengthen the encoded time intervals, and reduce the noise in the representations of the time intervals. These results suggest that neural oscillations play a role in the encoding of interval time, and modulating the neural oscillations by external stimulations affects the encoding.

In Study 3, I further investigated the effects of neural entrainment by tACS, using the Bayesian adaptive discrimination task and the recognition task. In the discrimination task, participants determined whether the comparison interval was longer or shorter than the standard interval. In the recognition task, participants judged whether the probe interval matched the standard interval. In both tasks, tACS was applied during the standard intervals. Electroencephalograms (EEGs) were recorded throughout the tasks. Contrary to my expectation, I found no significant behavioral effects of tACS and no convinced EEG evidence for neural entrainment induced by tACS. It thus raised a question to the robustness of the effects of tACS on the neural entrainment, and suggested a possibility that the effects of tACS observed in Study 2 may be limited to the reproduction task.

In summary, this thesis demonstrated that time intervals are represented in working memory as discrete items, and comparable to working memory for visual textures. Also, I showed that modulating neural oscillations by visual flickers or tACS changed reproduced durations and noises in the representations, suggesting that neural oscillations play a role in the encoding of time intervals. Although Study 3 suggested the effects of tACS may be weak or task-dependent, together with the results of Study 1 and 2, this thesis provides insights into the question of how the time dimension of the human mind becomes the conscious content in the human mind, as well as the neural oscillatory mechanisms underlying working memory of time intervals.