# The transient twinkle perception is induced by sequential presentation of stimuli that flicker at frequencies above the critical fusion frequency

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# Abstract

The critical fusion frequency (CFF) is a threshold that represents the temporal limits of the human visual system. If two flickering stimuli with equal subjective luminances are presented simultaneously at different locations, the CFF is the temporal frequency above which they cannot be distinguished. However, when the stimuli are presented sequentially at the same position, a transient twinkle can be perceived around the moment of the changeover. To investigate the mechanism underlying this transient twinkle perception (TTP), we independently manipulated the luminance contrast and temporal frequency of the flicker, as well as the inter-stimulus interval (ISI). We found that TTP was greater as the luminance step was larger, it was stably perceived for flicker frequencies up to 200 Hz, and it was robust for all ISIs if flicker frequencies were below 250 Hz. For 250 and 300 Hz flicker, TTP was attenuated in the condition that 1-frame and 2-frame ISIs were inserted. These results can be explained by a simple filtering model that TTP occurs if the temporal change in a weighted moving average of stimulus luminance exceeds a certain threshold. TTP gives additional evidence that human visual system can detect the transient change of flicker stimuli at much higher temporal frequency than the CFF, by averaging mechanism of luminance.

*Keywords*: critical fusion frequency, moving averaging, temporal processing, transient twinkle perception

# The transient twinkle perception is induced by sequential presentation of stimuli that flicker at frequencies above the critical fusion frequency

Critical fusion frequency (CFF) represents a temporal resolution limit of our visual processing. When we look at a stimulus flickering at a frequency higher than the CFF (above-CFF flicker), we only perceive a stationary field. Though sensitivity to flicker varies depending on retinal illuminance (Kelly, 1961), eccentricity (Rovamo & Raninen, 1984), stimulus size, and the duty ratio of the flicker (Emoto & Sugawara, 2012), the CFF is generally around 60 Hz (explaining why the refresh rate of consumer displays is set at 60 Hz or higher). On the other hand, some studies have reported neural entrainment to above-CFF stimuli. For example, steady state visually evoked potentials (SSVEPs) have been observed for above-CFF stimuli (Herrmann, 2001; Lyskov, Ponomarev, Sandstrom, Mild, & Medvedev, 1998; Ramos-Júnior, Celino, Rodor, Ribeiro, & Muller, 2011). In addition, a single flash of a half sinusoid can be detected at up to 600 Hz (Levinson, 1968).

Recently, an interesting phenomenon relevant to above-CFF stimuli has been reported: When two different above-CFF stimuli are sequentially presented, a transient flash is perceived (Cheadle, Parton, Muller, & Usher, 2011; van Diepen, Born, Souto, Gauch, & Kerzel, 2010). In these studies, two stimuli were presented sequentially at the same position; one was the “flicker stimulus” in which two different-luminance frames were alternatively presented, and the other was the “continuous stimulus” in which all frames had an identical luminance. These stimuli were presented with CRT monitor at above-CFF refresh rate[1]. As a result, flickering frequencies were below (e.g., 50 Hz) and above (e.g., 100 Hz) the CFF for the flicker and continuous stimuli, respectively. The subjective luminances of these stimuli were matched so that observers could not differentiate them when they were presented at the separate locations. When these stimuli were presented at the same location (Figure 1a), however, a transient “twinkle” was occasionally perceived (Cheadle et al., 2011; van Diepen et al., 2010). We call this phenomenon “transient twinkle perception” (TTP, Figure 1b). Similar phenomena had been mentioned in the classic studies with a point light (Bird & Mowbray, 1969; Forsyth & Brown, 1961; Mowbray & Bird, 1969; Sen, 1964).

---Insert Figure 1 about here---

Reports showed that the perceived luminance of the above-CFF flicker was identical to that of a non-flickering stimulus whose luminance was matched to the averaged luminance of the above-CFF flicker (Cheadle et al., 2011; van Diepen et al., 2010). This is well known as the Talbot-Plateau law (Nelson & Bartley, 1964; Stockman & Plummer, 1998). Following this law and because of the differences in physical luminance between the flickers, the temporally local average of stimulus luminance should deviate maximally from the global average of luminance around the time of transition between two above-CFF flicker (Figure 1c).

To avoid confusion, we define several terms regarding stimulus luminance.

1) Flicker amplitude is the difference in luminance between the two components of a flicker stimulus, i.e., peak-to-peak amplitude. Because a flicker stimulus consists of a bright component (we name it “ON frame”) and a dark component (“OFF frame”), the amount of flicker amplitude can be described by the difference between these frames. In this study, we set the luminance of ON and OFF frames independently (described in detail in Experiment 1). 2) Luminance step is the difference between a luminance component in flicker stimulus and that of continuous stimulus. The relationship between the flicker amplitude and the luminance step is illustrated in Figures 1c and 1d. A flicker stimulus with less flicker amplitude yields a smaller step and vice versa. As described above, the component in flicker stimuli can be classified as ON frame or OFF frame. Thus, we can also define two luminance steps, one for ON frame and the other for OFF frame. We call the former “positive luminance step” and the latter “negative luminance step.” Note that the concept of luminance step does not simply denote the difference in luminance between ON/OFF frames of flicker stimulus and continuous stimulus, but also is involved with their temporal proximity. That is, the positive (negative) luminance step means that continuous stimulus precedes or follows the ON (OFF) frame of flicker stimuli (Figure 1e).

We postulate that perceptual luminance is determined by the temporal moving average of the physical luminance of the stimuli. Under this assumption, the flicker and continuous stimuli would be both perceived as steady-state stimuli with the same perceptual luminance because the moving averages of their physical luminances are the same, which is consistent with the conventional view, i.e., Talbot-Plateau law (Nelson & Bartley, 1964; Stockman & Plummer, 1998). However, if the stimuli are sequentially presented, the moving average should deviate around the time of transition, and we hypothesize that this deviation of the moving average is a plausible cause of TTP (Figure 1c–1f). This hypothesis is consistent with Cheadle et al. (2011), which showed that TTP was attenuated when flicker amplitude was ramped down resulting in the smooth transition to the continuous stimuli, resulting in a small luminance step.

Several studies have dealt with TPP as an artifact of experimental procedures because the primary purpose of the studies was to examine whether or not stimuli flickering at the gamma band frequency (25–70 Hz) could trigger unconscious selective attention (Bauer, Cheadle, Parton, Muller, & Usher, 2009; Cheadle et al., 2011; van Diepen et al., 2010). Thus, the perceptual mechanism of TTP itself has not yet been directly investigated in these studies. Especially, though Cheadle et al. (2011) suggested that the luminance step would a significant factor of the transient twinkle, they did not actively manipulated its amount but used the same gradual transition between two stimuli. Thus, it is still unclear whether the amount of luminance step affected the occurrence of TTP. When the amount of luminance step is manipulated, the temporal average around the time of transition should be influenced directly

(Figure 1). This transient deviation can be calculated by using the temporal averaging model. Comparing the model output and the human perception for various luminance steps would tell us how the simple moving-average model can explain our luminance perception.

The primary objective of this paper was to address the effect of fluctuation of temporal luminance average on TTP. We conducted a simpler version of the experiment to investigate systematically the effect of the luminance step on TTP, and tested whether temporal averaging could consistently explain the TTP. We examined the effects of the deviation of moving average on TTP by manipulating the stimuli in a luminance dimension (Experiment 1) and in temporal dimension (Experiment 2).

# Experiment 1

## Materials and methods

**Participants.** Five naïve graduate students (all male) from the University of Electro-Communications and one of the authors (YN) participated in the experiments (age: 24.5 ± 3.78 years; range: 22–32 years). No participants had any neurological or visual disorders, and all had normal or corrected-to-normal vision. Five of the six participants were right-handed. Participants gave their written informed consent and all experimental protocols were reviewed and approved by the ethical committee of The University of Electro-Communications.

**Apparatus.** Stimuli were generated by Psychlops software (http://psychlops.sourceforge.jp/, see also Maruya et al., 2010) on a Precision T3500 Workstation (Dell, Inc., Round Rock, TX) with an independent GPU (Quadro FX 1800, NVIDIA Corp., Santa Clara, CA), and displayed on a 21-inch CRT monitor (GDM-F520, SONY Corp., Japan. Spatial resolution: 1024 × 768 pixels, refresh rate: 140, 150, or 170 Hz, depending on experimental condition). The monitor was gamma-corrected to obtain linear output of luminance. Experiments were conducted in a dark room lit only by the monitor, at a viewing distance of 87 cm obtained using a chin rest.

**Stimuli.** Stimuli were donut-like rings of different flickering frequencies presented on a gray background (50 cd/m$^2$). The diameter and width of the ring were 4.0 and 1.0 deg, respectively. As depicted in Figure 2a, the ring had a sinusoidal luminance profile of 0.5 cycle/deg whose minimum luminance was the same as the background (i.e., 50 cd/m$^2$) and the central hole (That is, the minimum luminance was always emerged at the inner/outer edges on the ring, and was constant irrespective of the maximum luminance on the ring). The maximum (peak) luminance of the sinusoidal profile was determined as follows. For continuous stimuli, the rings with an identical luminance profile were repeatedly presented in synchronization with the vertical sync of the CRT monitor. As described in Footnote[1], this stimulus was not perceived flickering though it flickered physically. The peak luminance of these rings was fixed to 65 cd/m$^2$ (resultantly, Michelson contrast was 0.13). On the other hand, the flicker stimulus was implemented as alternation of bright ring (ON frame) and dark ring (OFF frame) (Figure 2b). The peak luminance of the ON and OFF frames were adjusted during the experimental procedure (described below) so that the perceived luminance (visibility) of flicker stimulus was equal to those of the continuous stimulus. Note that within a single trial, the flicker amplitude remained constant, different from a previous study (Cheadle et al., 2011).

---Insert Figure 2 about here---

Frequencies of the flicker stimuli were set to 70, 75, or 85 Hz, by means of setting the refresh rate of the CRT monitor to 140, 150, or 170 Hz, respectively. The luminance combinations of ON and OFF frames were determined by the adaptive method described below.

In a trial of Experiment 1, continuous and flicker stimuli were sequentially presented at the identical position (i.e., the center of the screen). Note that a small fixation dot was presented at the center of the ring to prevent from eye movement.

**Determining the point of subjective equal luminance.** Before conducting the main experiment, we confirmed for each participant that visibility between continuous and flicker stimuli was the same. To this end, the point of subjective equal luminance (PSE) between the stimuli was measured individually by the PEST method (Taylor & Creelman, 1967) separately for each flicker frequency.

In this measurement, we manipulated the OFF frame of flicker stimuli: Six peak luminances (50.0, 52.5, 55.0, 57.5, 60.0, and 62.5 cd/m$^2$) were used. These conditions brought negative luminance steps of 15.0, 12.5, 10.0, 7.5, 5.0, and 2.5 cd/m$^2$, respectively. In each measurement block, one of the OFF-frame peak luminances was randomly chosen and it was fixed during the block. On the other hand, the peak luminance of the ON frame was initially set to 80.0 cd/m$^2$ (i.e., the positive luminance step was set to 15 cd/m$^2$) and adaptively adjusted following the PEST procedure, as follows.

In the first interval of a trial, the continuous stimulus was presented for 30 frames as the standard stimulus. After 200-ms blank, the flicker stimulus was presented for 30 frames as the comparison stimulus in the second interval. Note that the physical duration for both stimuli varied depending on the flicker frequency (refresh rate). After the presentation of the stimuli, participants indicated which interval included the brighter ring through a two-alternative forced choice (2AFC). When a participant answered that the latter (flicker) stimulus was brighter, the peak luminance of the ON frame in the next trial was lowered, and vice versa. The trials repeated until the adaptive step size was smaller than 1 cd/m$^2$ (the termination condition). The peak luminance of ON frame in the terminated trial was defined as the PSE luminance that induces the subjective equal visibility between the continuous and flicker stimuli. A PSE luminance obtained for each OFF-frame peak luminance was also defined as the positive step of the flicker stimulus in the main experiment. As we will show below, the size of positive step was almost identical to those of negative step.

**Procedure of main experiment.** In one trial of the main task, two stimuli intervals were sequentially presented, separated by a 400-ms blank frame. One interval (named “twinkle interval”) consisted of a 30-frame continuous stimulus followed by a 30-frame flicker stimulus. We expected that the twinkle interval could potentially generate TTP due to the switchover of stimuli. The other interval (named “non-twinkle interval”) was a 60-frame continuous stimulus. Two types of twinkle intervals were prepared: One consisted of the positive step and the other consisted of the negative step (Figure 1e). Order of the twinkle and non-twinkle intervals was counter-balanced, and randomly assigned. In one trial, one of the twinkle stimulus types was also randomly selected (Figure 2c). Participants were asked to indicate in which interval the twinkle could be perceived (2AFC). The experiment was presented in blocks that differed in flicker frequency (70, 75, or 85 Hz), and the block order was randomized among participants. In a block, each of the 24 experimental conditions (2 orders of twinkle/non-twinkle intervals × 2 types of twinkle stimuli (positive/negative steps) × 6 sizes of luminance step) was randomly presented 20 times, resulting in 480 trials per block.

**Procedure of a supplementary experiment.** A supplementary experiment was also conducted to test whether TTP was observed if the order of the continuous and flicker stimuli was reversed (the order was fixed in the main experiment). In this experiment, a 30-frame flicker stimulus and a 30-frame continuous stimulus were sequentially presented once and the order of flicker and continuous stimuli was randomized trial-to-trial. Flicker frequency was fixed to 85 Hz, and only positive-step stimulus was used (Figure 1e). The size of the luminance step was chosen from 15.0, 7.5 or 2.5 cd/m$^2$. Five of the six observers who experienced the main experiment participated, and the task was to answer whether or not TTP was perceived. Each of six experimental conditions (2 presentation orders × 3 sizes of luminance step) was randomly presented 20 times.

## Results

**Subjective luminance matching.** First, we present the PSE luminance of ON-frame luminance obtained by the PEST method. Figure 3a shows the inter-participant averages of the PSE luminance of ON frame for different OFF frame luminances, separated by flicker frequency. The red dashed line indicates the predicted PSE luminance satisfying the condition that ON and OFF frame have equal luminance step. The PSE luminance of ON frames were closely aligned to the dashed line, indicating that they increased linearly with the increase the luminance of OFF frame. It also suggests that the size of the positive step derived from ON frame should be equal to that of the negative step. Thus, hereafter we referred to as simply “luminance step” (instead of positive and negative luminance steps) when we mentioned the size of luminance step, except the discussion of the polarity of the step.

**Detection of the transient twinkle.** We calculated the proportion of trials that each observer chose the twinkle interval for each condition (TTP ratio) while data were collapsed over the twinkle/non-twinkle intervals. Figure 3b summarizes the inter-participant average TTP ratio for each experimental condition. TTP occurred less often for smaller luminance steps, while the flicker frequency and the type of twinkle stimuli apparently have little effect. A three-way ANOVA (the type of twinkle stimuli × luminance step × flicker frequency) revealed a significant main effect of luminance step, $F(5,25) = 37.69$, $p < .0001$, $\eta^2 = .50$, and significant interaction between luminance step and flicker frequency, $F(10,50) = 3.57$, $p = .0013$, $\eta^2 = .06$. A simple main effect of the flicker frequency was significant for luminance step of 2.5 cd/m$^2$, $F(2,10) = 7.78$, $p = .009$; multiple comparisons by Bonferroni revealed that the TTP ratio was significantly higher in 75- than 70-Hz conditions ($p < .05$, Bonferroni corrected). A simple main effect of the luminance step was also significant for each frequency, 70 Hz: $F(5,25) = 25.00$; 75 Hz: $F(5,25) = 14.95$; 85 Hz: $F(5,25) = 18.06$ (all *ps* < .0001). Multiple comparisons by Bonferroni revealed that in all frequency condition, TTP ratio for 15.0 and 12.5 cd/m$^2$ was significantly larger than those for 2.5 cd/m$^2$ (all *ps* < .05, Bonferroni corrected).

These results show that the little difference was found between two types of twinkle stimuli. Though the flicker frequencies would affect TTP ratio for smaller luminance steps, more decisive factor for TTP was the luminance step; a greater luminance step induced TTP more robustly.

**Effect of stimulus order.** Figure 3c shows the averaged perceived ratios of TTP, indicating that the presentation order of flicker and continuous stimuli had no effect on the occurrence of TTP. A two-way ANOVA supported this finding with no significant main effects for presentation order, $F(1,4) = 0.08$, $p = .79$, $\eta^2 < .01$ or the interaction, $F(2,8) = 0.32$, $p = .74$, $\eta^2 < .01$.

---Insert Figure 3 about here---

## Discussion

In this experiment, we examined the effect of luminance step on TTP by modulating the flicker amplitude of the flickering stimuli. In contrast to a study in which flicker amplitude was gradually decreased before the time of transition (Cheadle et al., 2011), here, the luminance step was switched instantaneously, which made directly investigating the effect of the luminance step possible. The result showed that the transient twinkle was more frequently induced by a larger luminance step (Figure 3b), indicating that luminance step should be a critical factor for the TTP. We also showed that the TTP occurs independently from the direction and polarity of the temporal luminance change (Figure 3b and 3c). These results support our hypothesis that the temporal change in moving average may be a primary cause of the TTP. Owing to the luminance step between the continuous and flicker stimuli, the temporal luminance average fluctuates around the time of transition, which could cause the TTP.

To examine further the validity of this view, we performed a simple computer simulation by MATLAB (MathWorks, Inc., Natick, MA) showing how the moving average changes for flicker stimuli over time. In the simulation, the moving average was implemented with a temporally symmetrical Gaussian window. Thus, the moving average can be described by the convolution of the luminance profile of the stimuli and Gaussian distribution function as follows:

$$m(t) = \sum_{t=0}^{t} g(\tau) l(t-\tau) \quad , \tag{1}$$

where *m*(*t*) indicates the moving average at a certain timing *t*, *g*(*t*) indicates Gaussian distribution function, and *l*(*t*) indicates the temporal luminance profile of the stimuli. Here, as an example of the simulation, we show the result of a moving average with 100-ms window width whose *SD* (of Gaussian distribution) was 12.5 ms. The deviation of the moving average was larger for the larger luminance step (Figure 4a).

---Insert Figure 4 about here---

Figure 4b summarizes the peak values of the moving average around the time of transition. We applied moving averages with various window widths ranged from 20 ms to 180 ms at 40 ms intervals (Figure 4b). The relationship between the luminance step and the deviation from the mean luminance ratio (DMR) in the Michelson contrast showed a common tendency such that the relative amount of deviation increased with larger luminance steps.

To investigate whether the TTP ratio could be explained by DMR, we transformed the DMR into the probabilistic value by applying the Gamma cumulative distributed function with a shape parameter $k$ and a scale parameter $\theta$. The function gives the relationship between the DMR and the simulated response of TTP. We estimated the window width of moving average and parameters $k$ and $\theta$ of the function to minimize the error between the averaged TTP ratio and the transformed probability (i.e., the simulated TTP ratio) by the least squares method. Errors were pooled across experimental conditions. The estimated window width, $k$ and $\theta$ were 120 ms, 1.17, and 0.36, respectively. We also calculated the $R^2$ to assess the goodness of fit of the estimated parameters of the function. The resulting $R^2$ were 0.975, 0.897, and 0.947 for 70 Hz, 75 Hz, and 85 Hz, respectively (Figure 5).

---Insert Figure 5 about here---

This similarity between the psychophysical experiment and the computer simulation were consistent with our view that TTP depends on how much the moving luminance average deviates from its long-term mean. In Experiment 2, we manipulated the deviation of moving average by combining the flicker stimuli with different frequencies and inserting extra OFF frames at the transition to test our moving average model in the temporal dimension.

## Experiment 2

In Experiment 1, we manipulated the difference in luminance between continuous stimulus and (components of) flicker stimulus (i.e., luminance step). The result showed that TTP ratio was higher with a greater luminance step. In a computer simulation, a local moving average model successfully replicated the occurrence of TTP for different sizes of luminance step. When the amount of the luminance step was sufficiently large, TTP could be induced irrespective of the temporal frequency of the stimuli.

If the moving average hypothesis is correct, however, the deviation of luminance average should be affected by not only the luminance step, but also the width of averaging window; if a large amount of luminance alternation would be included within the wide window, the deviation should not stand out from their long-term mean. Therefore, the window width for temporal averaging is an important parameter for TTP. In other words, the occurrence of TTP would be affected by how frequent luminance alternation is assigned within the widow.

To investigate the issue, we should manipulate the number of luminance alternation by changing the temporal frequencies between different flicker stimuli having the same flicker amplitude. The deviation of moving average can be induced by the temporal structure of a visual stimulus. When two flicker stimuli with different flickering frequency but with the same flicker amplitude (their luminances are perceived equal) are presented sequentially, the temporal moving average should deviate around the time of their transition since the number of ON and OFF frames changes between after and before the transition (cf. Bird & Mowbray, 1969; Mowbray & Bird, 1969). It also means that the amount of deviation should vary due to the duration of ON and OFF frames within a temporal window of moving average.

The result of Experiment 1 demonstrated the effect of the luminance deviation induced by the luminance step on TTP, however, it is unclear how the temporal characteristic affects the occurrence of TTP. In Experiment 2, therefore, we investigated TTP from the viewpoint of temporal characteristics, in order to further examine the validity of the moving average model. We presented two flicker stimuli having different flicker frequencies with the same flicker amplitude as described above. In addition, we also inserted additional OFF frames, i.e., inserting ISI frames in order to manipulate the temporal property of the stimulus. These manipulations should also induce the large deviation in moving average around the time of transition as well as those of manipulation of the flicker amplitude, i.e., the luminance step. If our hypothesis is correct, TTP could be observed even if the successive flicker stimuli with/without ISI are presented so far as a certain amount of deviation of luminance average arises around the time of transition. Moreover, we will conclude that TTP would occur due to the deviation of luminance average around the time of transition within a temporal averaging window.

For manipulating the temporal frequency of flicker stimuli and ISI, we adopted a high-speed DLP projector that can present binary images with a refresh rate up to 5000 Hz. Making use of this device, we could examine the effect of the deviation of moving average on TTP in high temporal frequency conditions which could not be examined with conventional CRT monitors as used in Experiment 1.

## Materials and methods

**Apparatus.** Stimuli were projected onto a distal screen (width 123.5 × height 93 cm, height from floor to bottom of screen 113 cm) using a high-speed DLP LED projector (DLP Light Commander, Texas Instruments, Inc. Dallas, TX. Spatial resolution: 1024 × 768 pixels) in a dark room. Five projector refresh-rates were used: 400, 600, 800, 1000, and 1200 Hz. Participants sat in a non-reclining chair about 200 cm from the screen. Each participant was asked to adjust the chair so that eye level matched the vertical center of the screen, and asked to straighten the spine against the back of the chair to maintain the correct eye position. No chin rest was used. The projector was controlled by Psychlops software (Maruya et al., 2010) and the API for the projector (distributed by Texas Instruments, Inc.) on a MacBook Pro (Apple, Inc. Cupertino, CA). To display the images, we first prepared 1-bit bitmap images and then converted them into the projector specific format (.dbi). Next, the converted images were sent into the memory of the projector in advance of starting the experimental session. During the experiment, the order of the pre-loaded images was controlled by the API.

**Participants.** Four graduate students in The University of Electro-Communications and author YN participated in the experiment (age: 26.6 ± 3.61 years, range: 23–33 years). Three of them had also participated in Experiment 1. None had neurological or visual disorders and all had normal or corrected-to-normal vision.

**Stimuli.** The stimulus configuration was the same as in Experiment 1, however because the stimuli were 1-bit bitmap images, each ring had a homogeneous luminance (white or black, Figure 6a). We modulated the sequence of white ring (W) and black ring (B) frames to display the flicker with different temporal frequencies, i.e., flicker stimuli with high temporal frequency (HTF stimuli) and that with low temporal frequency (LTF stimuli). Unlike the transient light emission on a CRT monitor, each ring was presented continuously over a frame. To distinguish the stimuli ring from the background spatially and temporally, 1-by-1 pixel white-and-black checkerboard patterns were presented on background, so that the perceived background luminance was mean luminance between white and black rings.

---Insert Figure 6 about here---

For stimuli flickering at high temporal frequencies (HTF stimuli), one flicker cycle was composed of four frames: WWWB or BWWW. For the stimuli at low temporal frequencies (LTF stimuli), one flicker cycle consisted of eight frames: WWWWWWBB or BBWWWWWW. Because each frame was displayed synchronously with the refresh rate of the projector, the flickering frequencies of HTF and LTF stimuli can be regarded as ¼ and ⅛ of the refresh frequency, respectively. Thus, the frequency of HTF stimuli was always twice as high as that of LTF stimuli. Five HTF stimulus frequencies were used: 100, 150, 200, 250, and 300 Hz, corresponding to the refresh rates of the projector, 400, 600, 800, 1000, and 1200 Hz, respectively. The duty ratios of HTF and LTF stimuli were both 75% (Figure 6b), meaning that in a single cycle the temporally averaged luminances of HTF and LTF stimuli were 75% of the white-frame luminance. The reason why we selected the 75% duty ratio was also due to only using the 1-bit bitmap images. If the flicker stimuli were assembled by a number of cycles consisting of the same number of W and B frames (i.e., 50% duty ratio), the averaged luminance of rings became the same as the background.

**Procedure of main experiment.** The general procedure was the same as Experiment 1. In each trial, two stimulus intervals (twinkle interval and non-twinkle interval, each lasting 320 ms) were presented sequentially (separated by 480 ms), and participants indicated which interval included the twinkle via a two-alternative forced choice. The twinkle interval was randomly assigned to either before or after the blank frame.

In the twinkle interval, HTF and LTF stimuli were sequentially presented. More specifically, we put a single black ring (B) frame between the two stimuli

(Figure 6c and 6d, top panel). We represent the frame sequence of the first stimulus as BWWW (HTF) or BBWWWWWW (LTF), and that of the following stimulus as WWWWWWBB (LTF) or WWWB (HTF). We call the former HTF-LTF stimuli and the latter LTF-HTF stimuli. The ISI between the two stimuli was fixed to one frame when a single B frame was inserted, and this was called the 1B-frame condition. We also included 2B- and 3B-frame conditions to manipulate ISI duration (Figure 6c and 6d, middle and bottom panels). The order of HTF and LTF stimuli in the twinkle interval was counterbalanced. Note that the absolute duration of the ISI for the 1B-frame condition changed depending on the refresh rate. In the non-twinkle interval, only HTF stimuli (WWWBWWWBWWWB…) were sequentially presented for 320 ms. The experiment was presented in blocks that differed in the flicker frequency, and block order was counterbalanced among participants. In a block, each of 12 experimental conditions (2 orders of twinkle intervals × 2 presentation orders for HTF/LTF stimuli × 3 ISIs) was randomly presented 10 times, yielding 120 trials per a block.

**Procedure to test the perceived luminances.** To confirm that the perceived luminances of HTF and LTF stimuli matched, we also conducted a temporal 2AFC experiment examining the difference in subjective luminance between these flickers. The standard stimulus was an HTF stimulus (as in the main experiment: 4 frames/cycle, 75% duty ratio, W:B = 3:1), and the comparison stimulus was a flickering ring of 8 frames/cycle. The duty ratio of the comparison stimulus was either 25, 62.5, 75, 82.5 or 100% (W:B = 2:6, 5:3, 6:2, 7:1, or 8:0, respectively). Here, the stimulus with 75% duty ratio was the same as the LTF stimuli and the other stimuli were fillers to ease the judgment of the task. The standard (comparison) stimulus was randomly assigned to either pre-interval (320 ms) or post-interval (320 ms), and the blank duration between intervals was 480 ms. The participants were asked to indicate which interval contained the brighter ring. This experiment was also presented in blocks that differed in flicker frequency of HTF stimuli. The block order was randomized among participants. In a block, ten trials were assigned for each condition, and thus the number of trials was 100 (2 intervals × 5 duty ratios of comparison stimuli × 10 trials).

## Results and Discussion

**The perceived luminance of HTF and LTF stimuli.** We calculated the proportion of trials that the comparison stimulus was brighter than the standard stimuli for each observer. Figure 7a shows the average response ratio among participants in the condition that the stimuli had the same duty ratio (75%). The result revealed that stimuli with identical duty ratios produced the same subjective luminance even if the temporal frequencies of flicker were different. This indicates that the perceptual luminance of HTF and LTF stimuli were successfully matched for each flicker frequency.

**TTP ratio for HTF/LTF stimuli.** We pooled the data from conditions with counterbalanced orders (twinkle/non-twinkle intervals and the presentation orders for HTF/LTF stimuli). We plotted the averaged TTP ratio among participants as a function of the number of black frames (Figure 7b). The panel shows that the TTP ratio was almost maximal in all ISI conditions up to 200 Hz, but was lower in 1B- and 2B-frame conditions than in the 3B-frame condition when the flicker frequency was greater than 250 Hz. Because duration of a single frame is varied by the refresh rate, we assumed that the TTP ratios might be plotted simply as the monotonically increasing function of the physical time, not the frame duration. Thus, we further re-plotted the result as a function of ISI in terms of physical time (Figure 7c). However, that assumption was not true. Specifically, although the TTP ratio was maintained high for ISI duration shorter than 2 ms in the condition of 150- or 200-Hz HTF, it markedly decreased when the frequency of HTF stimuli was 250 or 300 Hz. It suggests that physical time of ISI frames could not fully describe the occurrence of TTP.

---Insert Figure 7 about here---

A two-way ANOVA (flicker frequency × ISI) revealed that the interaction between the two conditions was significant, $F(8, 32) = 11.49$, $p < .0001$, $\eta^2 = .20$. The main effects of flicker frequency, $F(4, 16) = 23.97$, $p < .0001$, $\eta^2 = .40$, and ISI, $F(2, 8) = 33.95$, $p < .0001$, $\eta^2 = .22$, were also significant. Analysis of the simple main effect revealed a significant difference of TTP between ISIs for 250 Hz, $F(2, 8) = 26.53$, $p = .0003$, and for 300 Hz, $F(2, 8) = 18.40$, $p = .001$. A significant difference of TTP between flicker frequencies also emerged in 1B-frame ISI, *F*(4, 16) = 13.44, $p < .0001$, and 2B-frame ISI, *F*(4, 16) = 27.02, $p < .0001$, respectively. Multiple comparisons by Bonferroni for the difference of ISI in 250 and 300 Hz revealed that TTP ratios in 1B-frame and 2B-frame ISI conditions were significantly lower than 3B-frame conditions (all *ps* < .05, Bonferroni corrected). As for the difference between flicker frequencies in 1B- and 2B-frame ISI conditions, the TTP ratio for 250 and 300 Hz was significantly lower than the other frequency conditions (all *ps* < .05, Bonferroni corrected).

**Application of the moving average model.** To investigate the cause of the difference that occurred for ISI durations (Figure 7), we ran a computer simulation of the moving average for an HTF stimulus presented with different blank intervals (Figure 8a). The flicker frequency was chosen from 100, 120, 150, 200, 240, and 300 Hz. A positive deviation from the mean was observed around the time of transition in the 1B-frame condition while negative deviations were observed in 2B- and 3B-frame conditions. This polarity difference of deviation stemmed from the ratio between W and B frames within the window of moving average; the computational simulation for the HTF-LTF stimuli suggests that the stimulus around the transition contained more W frames than B frames in 1-B condition while it contained more B frames in 2-B and 3-B conditions. For every HTF stimulus the deviation size was smaller with higher flicker frequencies and with shorter ISIs.

---Insert Figure 8 about here---

The magnitudes of largest deviations in all conditions are summarized in Figure 8b. The vertical axes (deviation from mean luminance ratio: DMR) are plotted in a logarithmic scale. For each ISI, plotted lines were shifted parallel except the simulation with 20-ms window width. It indicates that the difference in DMR between frequencies was almost the same in a logarithmic scale. As in Experiment 1, we transformed DMR into the probabilistic value by applying the Gamma cumulative distributed function. The window width of moving average and parameters $k$ and $\theta$ were estimated by the least squares methods. Here the estimation was conducted for 100, 150, 200, and 300 Hz conditions because of the correspondence between the simulation and the psychophysical experiments. After the estimation, we applied the transformation to remaining frequency conditions with the estimated parameters. The estimated window width, $k$ and $\theta$ were 120 ms, 7.45, and 0.08, respectively. The $R^2$ for each estimated curve showed 0.9166, 0.997, 0.995, and 0.999 for 100, 150, 200, and 300 Hz respectively (Figure 9).

These results also support our hypothesis that TTP is induced when the moving average of luminance deviates from its long-term mean. The deviation is successfully transformed into DMR since the DMR was quite similar to the experimental result in both experiments, and procedures to obtain DMR were exactly same between the two experiments. It also implies that the detection of transient change in moving average might be implemented by two processing stages: Linear moving average and non-linear transformation.

--- Insert Figure 9 about here---

## General discussion

### Summary of results

In this paper, we focused on the transient twinkle perception (TTP) that occurs around the time of transition between two different stimuli having temporal frequencies higher than the critical fusion frequency (CFF). We showed that greater luminance step could enhance TTP (Experiment 1) and flicker up to 200 Hz (above the CFF) could induce TTP, while those above 200 Hz could not (Experiment 2). Additionally, for flicker stimuli of 250 and 300 Hz, TTP could be induced by inserting ISI frames between the flicker stimuli (3B-frame condition in Experiment 2). These characteristics of TTP were explained with a simple computational model consisting of a temporal-averaging filter and a non-linear transformation. Both altering the flicker amplitude and inserting ISIs between the stimuli caused the moving average around the time of transition to deviate significantly from the mean luminance, resulting in the TTP. Below, we discuss a possible mechanism for TTP from the viewpoint of the moving average in luminance perception.

### The explanation of the TTP by moving average model

The experiments demonstrated that the TTP was induced by the flicker stimuli at frequencies much higher than the CFF, successfully replicating results of other studies (Bird & Mowbray, 1969; Cheadle et al., 2011; Mowbray & Bird, 1969; van Diepen et al., 2010). Beyond this, our results show that the temporal limit for TTP might be around 200 Hz (Experiment 2). Our data clearly show that some kinds of percept could be obtained as a transient twinkle even for above-CFF stimuli.

One might argue that it is contradictory that transition from a 100-Hz flicker to a 200-Hz flicker can induce robust TTP whilst we cannot perceive a constant flicker at 100 Hz. This discrepancy can be resolved by the moving average model because the moving average depends on whether or not the transition occurs within the temporal range of averaging. For example, if a bright stimulus abruptly appears on a dark background, the moving average (around the stimulus onset) significantly increases, which induces "bright" perception. If the stimulus disappears, the average should decrease toward the background luminance, which induces "dark" perception. An intermittent repetition of this stimulus produces repetitive alternation of bright and dark (or background) luminance, leading to the perception of a flicker. With a wider window of temporal averaging, both ON and OFF frames are included in the averaging window and the temporal fluctuation becomes smaller. As an extreme, when the fluctuation is almost zero, we can no longer perceive the flicker. However, if luminances of the ON frames are different between the stimuli before/after the time of transition, then the average should fluctuate around the time of transition even when moving averages within individual flicker stimuli are stationary (and have identical values). Therefore, even if a moving average with a certain window width does not fluctuate for 100-Hz flicker, it could fluctuate at the switch from 100- to 200-Hz flicker.

We can think of several mechanisms for the TTP. Our visual system has not only low-pass temporal filter (i.e. the moving average operator), but also the band-pass temporal filter (Kelly, 1961, 1971; Rovamo, Raninen, & Donner, 1999). One might argue that a better model could be developed by means of combining these filters. Although the processing for the TTP might depend on these filters, our simple one-stage averaging model successfully can explain our experimental results (Figures 5 and 9). In our model, a moving average was calculated by averaging the raw (i.e., not-filtered) flicker stimuli up to 300 Hz. These above-CFF signals might be mediated by the filters in the visual system. As shown in the previous studies on SSVEP for above-CFF flicker (Herrmann, 2001; Lyskov et al., 1998; Ramos-Júnior et al., 2011), our visual system can show the neural response to these temporal signals irrespective of whether these responses leads to an explicit perception or only a behavior of the neural system. Related to this point, recent studies pointed out the contribution of above-CFF flicker for conscious perception; luminance contrast sensitivity function was shifted toward higher temporal frequency region after adaptation to flicker stimuli (Shady, MacLeod, & Fisher, 2004). Interestingly, the sensitivity was greater than those without adaptation even when the adaptation flicker was invisible (above-CFF) for observers. Johnston et al. (2008) reported the perceptual shrinkage of duration for 10-Hz flicker stimuli after the adaptation to above-CFF flicker, suggesting that this effect would be caused by the change in the magno cells in the retina and/or LGN. Although we cannot reach a definitive conclusion of the source of TTP, we can at least say that a one-stage moving average model with a nonlinear transformation can explain the TTP.

## The temporal characteristics for TTP

The result of Experiment 2 (Figure 9 left) suggests the existence of categorical difference of TTP ratio between 200-Hz and 250-Hz HTF in short ISI conditions. The simulation by the moving average model (Figure 9 right), however, simply showed a gradual decrease of the TTP ratio for these ISIs. This discrepancy might stem from the difference in the flicker frequency between the psychophysical experiments and the computer simulations; we used 100, 150, 200, 250, and 300 Hz in the psychophysical experiments while we chose 100, 120, 150, 200, 240, and 300 Hz for computational convenience. Comparing 240 Hz condition with 250 Hz condition, the TTP ratio was slightly lower in 250 Hz condition, indicating that the TTP ratio at short ISIs gradually decreases with higher flicker frequency.

Related to this issue, the temporal threshold for flicker perception might be much higher than what we have known. Recently, by using a similar high-speed device, Davis, Hsieh, and Lee (2015) reported that the above-CFF flicker stimulus could be perceived when it had edges with high spatial frequency; they showed that the contrast sensitivity for flicker stimulus gradually decreased up to around 400 Hz, and drastically dropped off over this frequency (Figure 3 of Davis et al., 2015). It suggests that our visual system might have another baseline for the temporal sensitivity above CFF frequency. When the flicker frequency of HFT stimuli was 300 Hz, average TTP ratio was slightly below the differential threshold (0.75) for the short ISIs, implying that 300 Hz might not be the temporal limit for TTP. Therefore, if we examine HTF stimuli with greater frequency than 300 Hz, we could find the temporal limit of TTP where the TTP ratio is at chance level (0.5). This topic is beyond the present scope, but the high-speed device would have a possibility to reveal the high-speed temporal processing that we have not found yet.

## Effects of below-CFF frequency components on TTP

Another possible cause of occurring TTP might be an existence of low-frequency components in our flicker stimuli. To test this, we applied FFT to the temporal luminance profile of stimuli and found that the power of below-CFF frequencies were surely included in above-CFF flicker stimuli; the power of each frequency component was not zero but was much lower than the maximum power in the stimuli (Figures 10 and 11). Note that below-CFF power exists in both HTF and

LTF stimuli themselves since our stimuli were rectangular flicker (cf. Figure3c of van Diepen et al., 2010).

---Insert Figures 10 and 11 about here---

Although this tendency was also found in each panel in the third column of Figure 11, TTP ratios in the condition of combination of 150-Hz LTF and 300-Hz HTF were significantly different (Figure 7c) regardless of the similarity between their spectrum profiles. Moreover, we should note that the flickering could not be perceived for either flicker (Experiment 1), HTF or LTF (Experiment 2) stimulus alone whilst these stimuli contain considerable power for below-CFF frequency region. This indicates that the existence of below-CFF frequency components could not directly linked to the stimulus perception, and thus, power of below-CFF frequency must not be the direct cause of the TTP.

**The perceived brightness of TTP**

If the moving average directly denotes the perceptual luminance, the nature of TTP might depend on the direction (or polarity) of deviation from mean luminance. Our results, however, did not support this idea. The result of Experiment 1 (Figures 3b and 3c) showed that TTP was consistently observed irrespective of the stimulus order (continuous → flicker, or flicker →continuous). Additionally, in Experiment 2, TTP occurred almost equally for positive and negative deviations (Figure 7). Computer simulation of the moving average model showed a good correspondence to these results when we calculated absolute value of deviation (Figures 5 and 9). A previous study reported that the perceived luminance of transient flash was varied among individuals; one could discriminate the brightness of a flash, and some could not (Mowbray, Flower, & Bird, 1975). We also confirmed that it was very hard even for an experienced observer to differentiate the TTP luminance induced by negative or positive luminance steps.

One possible explanation for this is that the important factor for TTP might be independent of the polarities of luminance changes. This view seems consistent with findings regarding perception of luminance change. First, Roufs (1974) indicates that incremental and decremental brief luminance flashes cannot be distinguished. Second, a decremental probe presented on a flickering background is perceived the same as an incremental probe (Wolfson & Graham, 2001). These findings support the idea that polarity of deviation does not greatly affect the perceived luminance of the TTP. This characteristic would be an advantage to detect the transient change in the environment as fast as possible without a careful examination of contents in the change. If, for TTP, our visual system might not be sensitive to the luminance polarity of deviation around the transition, the occurrence of TTP would be owing to the absolute variation from luminance average. The neural response for the transient and flicker signal should be shown in the magnocellular pathway (for a review, see Livingstone & Hubel, 1988). Thus, TTP, especially the detection of the deviated luminance average, might be processed in this pathway. Magno cells of macaque show the maximal sensitivity to 10-Hz flickering stimuli (Lee, Martin, & Valberg, 1989), whose frequency almost corresponds to the estimated window width of moving average (120 ms, 8.3 Hz). Further research is needed to test whether or not magnocelluar pathway processing would be related to TTP. For example, this issue will be resolved by applying the adaptation for flickering stimuli at various temporal frequencies before observation of TTP stimuli (cf. Chapman, Hoag, & Giaschi, 2004; Nieuwenhuis, Jepma, La Fors, & Olivers, 2008). If our estimated window width of moving average would reflect the temporal sensitivity of magnocelluar pathway, the adaptation for flickering stimuli at an optimal temporal frequency would impair the occurrence of TTP.

Another possible explanation of insensitivity for luminance polarity might be the low contrast (DMR) between the long-term average and the deviation of this average. Computational simulation for DMR (Figures 4b and 8b) and simulated TTP ratio (Figures 5 and 9) suggest that higher TTP ratio could be shown even for approximately 0.01 of DMR (Figure 4b and 8b). The amount of DMR almost corresponds to the highest temporal contrast sensitivity (cf. Kelly, 1961), indicating that the DMR would be near the detection threshold level. If the luminance deviation around the stimuli transition is quite different from the long-term averaged luminance, observers might distinguish the polarity of TTP. For example, we could modify the flicker stimuli used in Experiment 1; if the luminance of OFF frame is lower than the background luminance, we could display the flicker stimuli with the larger amplitude than that in Experiment 1, i.e., the large luminance step could be presented. In this sense, the sensitivity for the polarity of deviation might depend on the polarity of the component luminance of flicker stimuli relative to the background: Whether the component luminance is across the luminance of background might be critical. In any case, in our experiments TTP ratio for the positive and negative deviations did not show any differences. It suggests that the polarity of the deviation does not affect the occurrence of TTP. If any, it would not contribute to the luminance perception for TTP, but to telling the emergence of deviation itself.

In summary, although we cannot conclude whether TTP may or may not be accompanied by the brightness perception, the important factor for the TTP is whether a sufficient amount of temporal change in the moving average emerges around the time of transition.

## Conclusions

The present study showed that TTP was dependent on the size of the luminance step at the transition between stimuli having different luminance components. The larger luminance step results in the larger temporal deviation from the long-term luminance mean. The degree of temporal deviation could explain this phenomenon. The temporal deviation should also be brought about by the successive flicker stimuli with different temporal frequencies. The perception of transient twinkles is determined by whether or not the amount of moving luminance average around the transition exceeds a certain threshold.

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## Footnotes

[1] A CRT monitor generates a very short light impulse (< 1 ms) at the beginning of every frame. Thus, for most of the frame, no light is physically emitted, even when the bright frames are presented synchronously with the v-sync of a CRT. This means that the “continuous stimuli” are technically not presented continuously, although for convenience we call this type of stimuli “continuous” to differentiate them from the “flicker” stimuli.

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**Figure captions**

Figure 1. The transient twinkle perceived when continuous and flicker stimuli are presented sequentially. (a) A flicker stimulus and a continuous stimulus are presented sequentially without an inter-stimulus interval. (b) Even if these stimuli bring the same perceptual luminance, a brief luminance change (i.e., a transient twinkle) can be perceived just around the time of transition. (c) When the moving average is calculated for the stimuli like (a) with an averaging window, the average at the transition should deviate from that before/after the transition as plotted in the side box. The smaller luminance step (d) leads to less temporal change of moving average around the time of transition. The two types of luminance step (positive/negative) are shown in (e). The polarity of the step was defined by which luminance component (ON/OFF frame) in the flicker stimulus was adjacent to the continuous stimulus.

Figure 2. Schematic diagrams of the stimuli used in Experiment 1. Rings whose luminance had a half-rectified sinusoidal profile were used as stimuli (a). The flicker stimulus (b, left) consisted of a bright ring (ON frame) and a dark ring (OFF frame) presented alternately while the continuous stimulus (b, right) was a stationary illuminant ring. The luminance steps were manipulated by modulating the luminance of the ON and OFF frames (c). To equalize the perceptual luminance between flicker and continuous stimuli, the luminance of ON frame was estimated by the PEST

method, separately for individual OFF-frame conditions and participants. The size of luminance step can be defined by the difference between an OFF (ON) frame of flicker stimuli and a luminance component of continuous stimuli. In (c), only negative luminance steps of 15, 7.5, and 2.5 cd/m$^2$ were shown (cf. Figure 1e).

Figure 3. Results of Experiment 1. (a) Results of subjective luminance matching by the PEST method. The lower horizontal axis indicates the luminance of the OFF frame of flicker stimulus. The left vertical axis indicates the matched luminance of ON frame. The red dashed line indicates the case in which the luminances between OFF frame ON frame are equal. The corresponding size of positive (the right vertical axis) and negative (the upper horizontal axis) steps is also shown. These sizes are defined by the difference between luminance of continuous stimulus (= 65 cd/m$^2$) and luminance of the ON/OFF frame of flicker stimulus. (b) Results of the main experiment. The averaged TTP ratios (the ratio that participants chose the twinkle interval) are plotted as a function of the luminance step. (c) The effect of stimulus (flicker or continuous) presentation order. The horizontal axis indicates the size of luminance step and the vertical axis indicates the perceived ratio of the transient twinkle. Error bars in each panel indicate standard error of mean.

Figure 4. Results of computer simulation of the moving average model. (a) Thin gray line in each panel indicates the simulated luminance profile of 85-Hz flicker stimuli. We applied moving average (details were described in the main text) to the luminance profile and the output is plotted with thick curves. Rows indicate different luminance steps, and columns indicate different stimulus transitions (i.e., combinations of different stimulus orders and different step polarities). (b) Contrast between the deviation of the moving average and the mean luminance. Averaging windows had Gaussian profiles with different temporal widths ranged from 20 ms to 180 ms at 40 ms intervals. The horizontal axes indicate the size of luminance step and the vertical axes indicate the log contrast between the deviation and mean luminance (deviation from the mean luminance ratio: DMR). The magnitude of the deviation was estimated by the mean deviation from the mean luminance between 250 and 350 ms after the transition. Though this figure only shows the results in the condition that the stimulus order was from continuous to flicker stimulus and the luminance-step polarity was positive, the same tendency was observed with reversed stimulus order and with negative luminance steps.

Figure 5. Transformation of DMR (Experiment 1). The left panel indicates the results of Experiment 1 as a function of luminance step. Error bars indicate the standard error

of mean. The right panel indicates the transformed DMR (simulated TTP ratio) by applying the Gamma cumulative distribution function with optimized parameters.

Figure 6. Stimuli used in Experiment 2. We used homogeneously luminant white and black rings. The background of each stimulus was a checkerboard pattern of 1 × 1 pixels (a). Owing to the high-speed DLP projector, each frame was displayed at a much higher refresh rate than is possible on a CRT monitor, resulting in the temporal frequency of the flicker being one *n*th of the refresh rate (b). One flicker cycle composed four (top, HTF stimuli) or eight (b, LTF stimuli) frames. The white and black rectangles below each luminance profile indicate the number (duration) of white and black rings per a cycle in each condition. (c) and (d) indicate manipulation of the ISI between HTF and LTF stimuli: We inserted additional black ring frames (B) at the transition between HFT and LTF stimuli.

Figure 7. Results of Experiment 2. (a) Results of the comparison experiment for luminance between HTF (standard) and LTF (comparison) stimuli. The dashed horizontal line indicates chance level. (b) Averaged TTP ratios are plotted as a function of the number of ISI frames. (c) They are re-plotted as a function of the absolute duration of additional black frames. Error bars in all graphs indicate the standard error of mean.

Figure 8. Results of the computer simulation of moving average for HTF and LTF flickers. (a) Thin gray lines in the panels indicate the simulated luminance profile of 100, 150, 200, and 300-Hz HTF stimulus. We applied moving average to the profile, and the result was plotted with thick curves. Rows denote the frequencies of HTF stimuli, and columns indicate the ISI frame-number. (b) Deviation of the moving average. To obtain DMR, we performed the same procedure that was used for producing Figure 4. The horizontal axes indicate the number of ISI frames and the vertical axes indicate DMR.

Figure 9. Transformation of DMR (Experiment 2). The left panel indicates the results of Experiment 2 (the same as Figure 7b), and the right panel indicates the transformed DMR (simulated TTP ratio) by applying the Gamma cumulative distribution function with optimized parameters. Note that the conditions of 120 and 240 Hz were not used in Experiment 2.

Figure 10. The spectrum power of stimuli (Experiment 1). We applied FFT (with Hanning window) to the temporal luminance profile of the stimuli used in Experiment 1 (cf. gray lines in Figure 4a). Rows indicate different flicker frequencies, and columns

indicate different luminance steps. The horizontal and vertical axes of each panel indicate the frequency and the spectrum power, respectively.

Figure 11. The spectrum power of stimuli (Experiment 2). We applied FFT to the temporal luminance profile of the stimuli used in Experiment 2 (cf. gray lines in Figure8a). Rows indicate different LTF-HTF combination, and columns indicate different ISI frames. The horizontal and vertical axes of each panel indicate the frequency and the spectrum power, respectively.