Time dilation in a perceptually jittering dot pattern

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Although it is known that a moving stimulus appears to dilate in duration compared to a stationary stimulus, whether subjective motion devoid of stimulus motion is sufficient remains unknown. To elucidate this, we used a motion illusion in which an actually static stimulus clearly appears to move, a useful dissociation between actual and subjective motions. We used the jitter aftereffect resulting from adaptation to dynamic noise as such a tool and measured subjective durations of a static random-dot pattern in which illusory jitter was seen, an actually oscillating pattern mimicking the illusory jitter, and a static pattern without illusory jitter. Pattern oscillation as tiny as fixational eye movements robustly evoked time dilation, and time dilation to a similar extent was also induced by an actually static but subjectively jittering pattern. Taken together with the previous knowledge that this subjective jitter is related to a visually based compensation of spurious retinal image motions due to fixational eye movements, these findings demonstrate that visual duration computation is influenced by a representation at a high-level motion processing stage at which a stable visual world despite jittery retinal inputs has been established.

Introduction

We can easily be aware and make use of time to accomplish everyday chores, skillful athletic performances, speech, and music, just to name a few. In actuality, however, we must solve this seemingly easy task of knowing time without any hardwired sense organs specifically evolved to sense physical energy corresponding to the concept of time itself. It is likely that we have conscious awareness of time as a result of integrative processes. As evidence for the integrative nature of time processing, our perception of time can be strikingly elusive in the influence of many factors, such as attention (Casini & Macar, 1997; Cicchini & Morrone, 2009; Herbst, van der Meer, & Busch, 2012; Lejeune, 1998; Seifried & Ulrich, 2011; Tse, Intriligator, Rivest, & Cavanagh, 2004), arousal (Stetson, Fiesta, & Eagleman, 2007), expectancy (Pariyadath & Eagleman, 2007, 2008; Schindel, Rowlands, & Arnold, 2011; Ulrich, Nitschke, & Rammsayer, 2006), order (Hellström, 1985), size (Ono & Kawahara, 2007; Ono & Kitazawa, 2009; Rammsayer & Verner, 2014), and a variety of sensory signals, including visual dynamics. One of the most representative time illusions related to visual dynamics is adaptation-induced time compression (Johnston, Arnold, & Nishida, 2006), which demonstrates that adaptation to rapid flicker reduces the subjective duration of a subsequently presented stimulus. Another striking example is illusory time dilation of dynamic visual events (Kanai, Paffen, Hogendoorn, & Verstraten, 2006; Kaneko & Murakami, 2009), which is the target of this study. In a variety of situations, moving or flickering visual stimuli appear to last longer than their stationary counterparts.

In a duration range shorter than a few seconds, these time illusions have been extensively investigated to uncover possible underlying mechanisms by comparing

psychological characteristics with the knowledge of computational theories as well as visual neurosciences. In particular, findings from examinations of adaptation-induced time compression point to very early visual processing stages, perhaps earlier than the primary visual cortex. This illusion is severely restricted to the adapted spatial region in terms of retinotopy (Ayhan, Bruno, Nishida, & Johnston, 2009; Bruno, Ayhan, & Johnston, 2010; Johnston et al., 2006; Johnston, Bruno, & Ayhan, 2011; but see Burr, Cicchini, Arrighi, & Morrone, 2011; Burr, Tozzi, & Morrone, 2007), has no orientation tuning (Johnston et al., 2006), does not transfer between eyes (Bruno et al., 2010), can be induced by flicker that is neurally receivable but too rapid to resolve consciously (Johnston et al., 2008), and cannot be induced by equiluminant flicker (Ayhan, Bruno, Nishida, & Johnston, 2011). All of these points suggest major involvement of the magnocellular cells in the lateral geniculate nucleus (LGN) or its early recipient.

Time dilation in a dynamic stimulus, on the other hand, occurs in diverse experimental situations. Classical demonstrations of time dilation used solitary figures moved in a readily discernible trajectory (Roelofs & Zeeman, 1951), and a number of explanations were compatible with the time dilation there. Since then, many situations have been tested, and basic knowledge has been accumulated; time dilation occurs in multiple objects moving in unpredictable trajectories (Brown, 1995), in biological motion (Wang & Jiang, 2012), and in patterned stimuli such as random-dot kinematograms in sufficiently high coherence and drifting sinusoidal gratings (Bruno, Ayhan, & Johnston, 2012; Kanai et al., 2006; Kanai & Watanabe, 2006; Kaneko & Murakami, 2009; K. Sasaki, Yamamoto, & Miura, 2013). The last circumstance offers an intriguing situation because the drifting sinusoid comprises a temporal frequency and a spatial frequency, and their ratio is equal to the speed. Is the time dilation in the drifting sinusoid determined by temporal frequency or speed? The answer may depend on configuration; an expansive concentric grating appears to obey temporal frequency or flicker rate (Kanai et al., 2006) whereas a linear grating reportedly dilates as a function of speed (Kaneko & Murakami, 2009). The temporal frequency dependence is not incompatible with early process accounts whereas the speed dependence requires more complex processing because explicit speed tuning in neurons is found only in higher-tier visual areas, such as area MT/V5 (Perrone & Thiele, 2002; Priebe, Cassanello, & Lisberger, 2003; Priebe & Lisberger, 2004).

In more complex stimuli, interesting speed dependencies have been reported. When blobs were rotating about fixation, their rotational frequency or angular velocity, rather than their local speed, predicted time dilation (Linares & Gorea, 2015). A drifting plaid or a linear sum of two drifting sinusoids in different orientations appeared to dilate with increasing pattern speed rather than component speed when an integrated percept as a coherent pattern motion was consciously experienced (Yamamoto & Miura, 2012a). When perceived speed changed with perceptual organization of a moving diamond-shaped figure, perceived duration changed consistently (Yamamoto, 2016). When environmental and retinal motions were dissociated from each other through execution of smooth pursuit eye movement concomitant with stimulus motion, time dilation was more consistent with the environmental motion (Au, Ono, & Watanabe, 2012). Furthermore, when the phenomenon of motion contrast enhanced the subjective speed of a moving stimulus, the subjective duration was also enhanced (Gorea & Kim, 2015). In addition, recent studies reported complex influences of acceleration, deceleration, and other temporal changes of speed (Binetti, Lecce, & Doricchi, 2012; Bruno et al., 2012; Matthews, 2011; K. Sasaki et al., 2013). These findings suggest that perceived motion as an outcome of complex motion processing is the determinant factor of motion-induced time dilation.

To elucidate the importance of perceived as opposed to stimulus motion, we examined whether time dilation depends on the occurrence of motion perception from identical retinal stimulation. For time dilation to occur, is it sufficient to have perceived motion as a result of visual motion processing even devoid of stimulus motion? To address this question, illusory motion offers an ideal dissociation between retinal input and perception. However, it is difficult to use conventional motion illusions, such as induced motion and the motion aftereffect, for this purpose. Induced motion in a static stimulus requires simultaneous presentation of an inducing motion stimulus in its surround and usually appears to move more slowly than the inducer (Takemura & Murakami, 2010); thus, duration judgment may also be influenced by the presence of the moving inducer. The motion aftereffect perceived in a static stimulus after adaptation to a motion stimulus imposes another problem of presenting a static stimulus within the adapted retinal region where the functionality related to time as well as motion processing may be impaired (Curran & Benton, 2012). To escape these difficulties, we focused on the jitter aftereffect phenomenon, which is a robust and vivid subjective experience of tiny oscillatory motions in an actually static visual pattern (Murakami & Cavanagh, 1998, 2001).

An adaptation paradigm is used to produce this illusion. After prolonged exposure to a dynamic random-dot pattern with a sufficiently high refresh rate, static random-dot patterns are presented in the adapted region and its vicinity, and the latter pattern in

the previously unadapted region appears to move in random directions for a few seconds. It is revealed that this illusory motion reflects the observer's own small fixational eye movements, which occur continually while viewing the static dot patterns (Murakami & Cavanagh, 1998).

Note that the jitter aftereffect offers a suitable dissociation between actual and phenomenal motions because no moving stimuli are actually presented during the experience of the illusion and because motion is perceived within a static pattern presented in a region that has never been exposed to stimulus motion. Whatever mechanism might mediate the jitter aftereffect, interrelationship between its underlying mechanism and that underlying time dilation would be elucidated by examining whether time dilation occurs when subjective motion is seen or whether mere subjective experience of jitter in the static stimulus is ineffective at producing time dilation. Some clue to metric relationship might also be found by comparing a stronger jitter with a weaker jitter in terms of impact in producing time dilation. In addition, it is in itself important to examine whether time dilation occurs at all in a scene of randomly jittering motions, whether actual or phenomenal, because no previous study has empirically examined time dilation in pattern oscillations as tiny as retinal image motions due to small eye movements during fixation.

Methods

Observers

Eleven adults (five females; 19–23 years of age), including the first author and 10 observers who were naïve to the experimental purpose, participated in all experiments. All had normal or corrected-to-normal visual acuity. This study followed the guidelines of the Declaration of Helsinki and was approved by the institutional ethics committee of the Graduate School of the Humanities and Sociology of the University of Tokyo. The methods were carried out in accordance with the approved guidelines. Each observer gave written informed consent prior to the experiments.

Apparatus

In a dark room, stimuli were presented on a 22-in. CRT monitor (Mitsubishi Electric RDF223G; 1600 × 1200 pixels; refresh rate 75 Hz) controlled by a computer (Apple Mac Pro). Luminance linearity was corrected for the gamma profile measured by a monitor-attachable colorimeter (Cambridge Research System ColorCAL). All stimuli were generated using Matlab (MathWorks) and the Psychophysics Toolbox extensions (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997).

Stimuli and procedure

The purpose of the main experiment was to identify the duration at the point of subjective equality (PSE) on the basis of duration comparison performances. Each trial was mainly composed of three sequential stimuli: adaptation, test, and comparison (Figure 1). The adaptation and test stimuli were presented at 9° eccentricity to the right of fixation whereas the comparison stimulus was at 9° eccentricity to the left. A yellow fixation point was provided at the center of the monitor throughout the experiment. Stimuli were observed with both eyes open from a distance of 56 cm constrained by a chin rest.

The adaptation stimulus had a central region (7.5° in diameter) filled with a static random-dot pattern and a surrounding region (7.5° in inner diameter and 15° in outer diameter) filled with a dynamic random-dot pattern in a concentric configuration. Each region was densely occupied by square dots, each subtending 9 min × 9 min, displayed in black or white with 50% probability on a gray background (32.9 cd/m^2) at 99% Michelson contrast. The central pattern maintained the same random-dot pattern throughout the adaptation period whereas the surrounding pattern was refreshed to a new pattern at a frequency that will be specified later in the description of each condition.

The adaptation period was followed by an inter-stimulus interval chosen randomly from a range of 0–0.1 s, during which the surrounding region was filled with a static random-dot pattern while the central region was left blank at the background luminance. In the subsequent test period, the random-dot pattern in the central region was turned on, remained for 1.2 s, and disappeared. The contrast onset and offset were both blurred by half a cycle (0.2 s each, inclusive within the overall duration of 1.2 s) of a raised-cosine temporal window at 2.5 Hz with a contrast range of 0%–99%. The cessation of the central pattern was followed by an interstimulus interval chosen randomly from a range of 0.3–0.6 s and then by the comparison period, during which a comparison stimulus was presented in the left hemifield for one out of seven durations (0.64, 0.88, 1.04, 1.2, 1.36, 1.52, and 1.76 s) chosen in random order. The comparison stimulus was a static random-dot pattern presented within a circular region (7.5° in diameter). The onset and offset of the comparison stimulus were contrast-modulated with the same temporal window as described above. These contrast manipulations were introduced to discourage a

(A)

(B)

Adaptation
(5 s or 10 s)

Inter-stimulus
interval
(0–0.1 s)

Test
(1.2 s)

Inter-stimulus
interval
(0.3–0.6 s)

Comparison
(0.64,
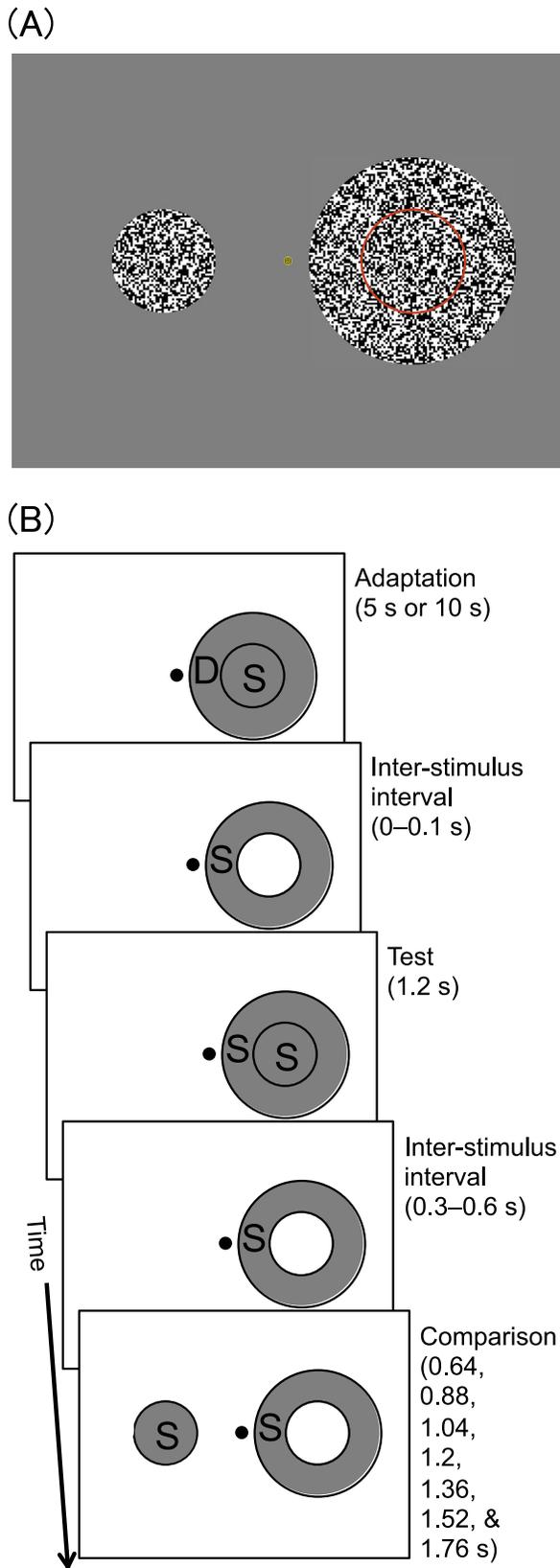0.88,
1.04,
1.2,
1.36,
1.52, &
1.76 s)

Time

Figure 1. Stimulus configuration. (A) A screenshot of the stimulus. The right- and left-hand stimuli are shown in the same frame for illustrative purposes; they never appeared at the same time in the experiment. The red circle is also shown for illustrative purposes here. (B) Schematic sequence of a duration comparison trial. "D" and "S" denote dynamic and static random-dot patterns, respectively.

strategy of focusing upon the onset and offset events as temporal cues from which the duration could be deduced.

Each observer was asked to judge which stimulus (test or comparison) appeared to last longer by pressing one of two keys on a computer keyboard. The observer's response immediately triggered the next trial.

There were five conditions: *baseline*, *jitter_full*, *jitter_half*, *real_full*, and *real_half*. In the *baseline* condition, the surrounding pattern was refreshed with an interpattern interval chosen randomly from a range of 0.6–1.4 s. After adaptation for 10 s to the pattern refreshed at this slow rate, a subsequently presented static pattern in the center yielded no illusory jitter perception. Thus, each observer compared the subjective duration of the actually and perceptually static pattern in the test stimulus with that of the comparison stimulus. This condition revealed each observer's baseline performance containing a constant error originating from several factors, including presentation order and location.

In the *jitter_full* condition, we attempted to produce a strong jitter aftereffect. To this end, we refreshed the surrounding pattern in the adaptation stimulus every display frame so that there were 75 uncorrelated patterns per second. This was the very adaptation condition used in the original report of the jitter aftereffect by Murakami and Cavanagh (1998). After adaptation for 10 s to this dynamic surround, the central static pattern in the test stimulus appeared to jitter vigorously in random directions. However, the jitter perception was experienced only during the presentation of the central pattern for 1.2 s; the illusion occurred only when a patterned static stimulus was presented in the central region—that is, the vicinity of the previously adapted region in the visual field. Thus, the observer's report on duration was based on what was seen in the central stimulus that was visible within this physical duration of 1.2 s.

The *jitter_half* condition was the same as the *jitter_full* condition except that the adaptation interval was halved to 5 s. Because a strong aftereffect occurs after a long exposure time of the adaptation stimulus, we expected this condition to yield a weaker jitter aftereffect.

The *real_full* condition had the same adaptation stimulus for the same interval as used in the *baseline* condition so that no aftereffect was produced. However, during the test period, the test stimulus was not static but physically moved back and forth in a

horizontal or vertical direction chosen randomly; every 10 display frames, the overall pattern was abruptly shifted by 3 min either horizontally or vertically, stayed stationary for five frames, and then returned to the original position and stayed for five frames. This animation of random movement within the central region looked very much like what one sees in the jitter aftereffect. Therefore, this condition was used to quantify the subjective duration of an actually moving stimulus that mimicked the appearance of the illusory jitter.

The *real_half* condition was introduced to examine the subjective duration of an actually moving stimulus at reduced oscillation amplitude. Thus, this condition was identical to the condition above except that the shift amplitude was halved to 1.5 min.

These five conditions were tested in separate experimental blocks in the method of constant stimuli. With 25% probability, within each block, we randomly interspersed dummy trials with the test stimulus duration chosen randomly from 0.8–1.6 s to discourage a strategy of referring to some representative duration of the test stimulus in the observer's memory that might have been formed gradually through repetitive trials if only one test duration had been consistently used within each block. The observer's responses to the dummy trials were excluded from the analysis. Each observer conducted multiple blocks until at least 24 repetitive trials were collected for each comparison duration for each condition. The order of blocks was counterbalanced.

The proportion of trials in which the comparison stimulus was reported to last longer was used to plot a psychometric function against the comparison stimulus duration and was fitted with a cumulative Gaussian by the maximum likelihood method using the Palamedes toolbox extensions for Matlab (Prins & Kingdom, 2009). The optimization allowed the cumulative Gaussian's mean and standard deviation (σ) to vary for each condition for each observer, and the lapse rate was fixed at 0.02 for both floor and ceiling (Prins, 2012).

Magnitude estimation and cessation timing of the jitter aftereffect

In separate experiments, all observers performed magnitude estimation about the subjective strength of motion under the *jitter_full* and *jitter_half* conditions. Each observer was instructed to report a magnitude in reference to the test stimulus in the *real_full* condition, which had been assigned "50" by the experimenter and to which each observer had been familiarized through repetitive observations in advance. The estimation had to be based on the motion strength felt at the beginning of the test stimulus. As in the main experiment, the

adaptation period was followed by the test period, but the test stimulus remained on the display until the observer pressed a key to indicate the cessation of motion perception, thereby timing the occurrence of the jitter aftereffect. Upon this reaction, the display turned blank with a text prompt asking the observer to enter a magnitude estimate via a number pad on the computer keyboard. There were 20 trials for each condition.

Magnitude estimation of the real oscillation

Magnitude was also estimated for the *real_full* and *real_half* conditions in a separate experiment. No adaptation period was involved; the central oscillating pattern in the test period for the *real_full* condition of the main experiment was presented 9° to the right for 1.2 s. Next, the central oscillating pattern of the test stimulus used in either the *real_full* or *real_half* condition of the main experiment was presented 9° to the left, also for 1.2 s. The observer was asked to report the magnitude of the second stimulus in reference to the first stimulus, which had been assigned "50" by the experimenter. There were 20 trials.

Results

The subjective duration of a random-dot pattern presented after adaptation to a dynamic random-dot pattern was compared with that of a subsequently presented random-dot pattern in the opposite hemifield to identify the duration at the PSE using essentially the same protocol across conditions.

Baseline as containing a constant error

Under the *baseline* condition, the PSE averaged across observers was significantly shorter than the veridical duration (two-tailed *t* test), $t(10) = 5.07$, $p < 0.0005$—that is, the static test stimulus that actually lasted for 1.2 s was judged to have the same duration as the static comparison stimulus that actually lasted for approximately 1 s (Figure 2). This underestimation can be explained by the well-known effect called time-order error that originated from the test stimulus always preceding the comparison stimulus (Hellström, 1985). Negative time-order errors, as observed here, have often been reported for durations longer than 1 s (Hellström, 1979, 2003) although positive errors have also been reported for shorter durations (Kanai & Watanabe, 2006; Pariyadath & Eagleman, 2007). Another possible factor contributing to the constant
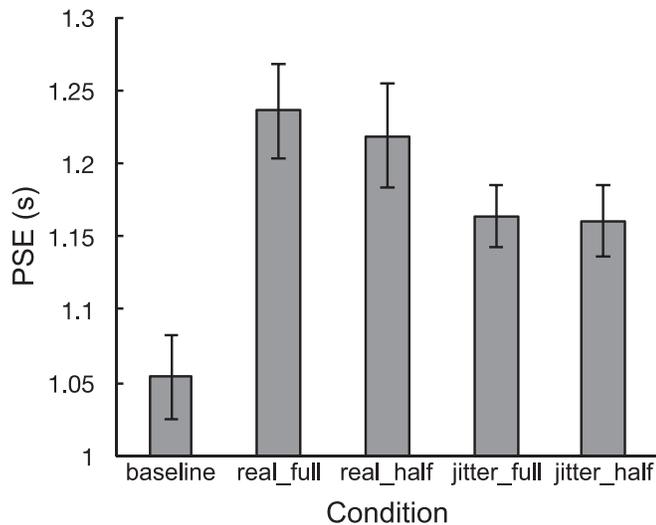
Figure 2. Averaged PSE plotted against condition. The upward direction of the ordinate indicates that the test stimulus appeared to last longer. Error bars indicate ±1 *SE*.

error may have been spatial anisotropy such that stimuli in one hemifield may appear to last longer than stimuli in the other hemifield (Vicario et al., 2008). On the other hand, perceived contrast cannot explain the constant error because the test stimulus did not appear to be artificially dimmer than the comparison stimulus and because it was confirmed that duration appeared stable even if physical contrast was halved. Nevertheless, the direction and mechanism of the constant error is out of scope here; this condition was deliberately introduced to quantify the baseline performance naturally containing a constant error that must be consistent across conditions. In reference to this baseline, further errors in duration perception are described below.

Real oscillation

Did time dilation occur when a stimulus actually oscillated on the display? The *real_full* and *real_half* conditions were introduced to mimic the perception of the illusory jitter by coherent oscillation of the dot pattern. Introspection from the observers confirmed that its appearance was similar to, although not indistinguishable from, the illusory jitter. Compared with the *real_full* condition, the *real_half* condition had half the oscillation amplitude. Indeed, in a separate experiment, we confirmed that the magnitude estimates under the *real_full* (58.5 ± 1.1) and *real_half* (42.5 ± 1.5) (mean ±1 *SE*) conditions differed significantly from each other, $t(10) = 12.61$, $p < 0.0001$ (Figure 3A).

In the main experiment quantifying the subjective duration, the PSE data under the *real_full* and *real_half* conditions were greater than under the *baseline*
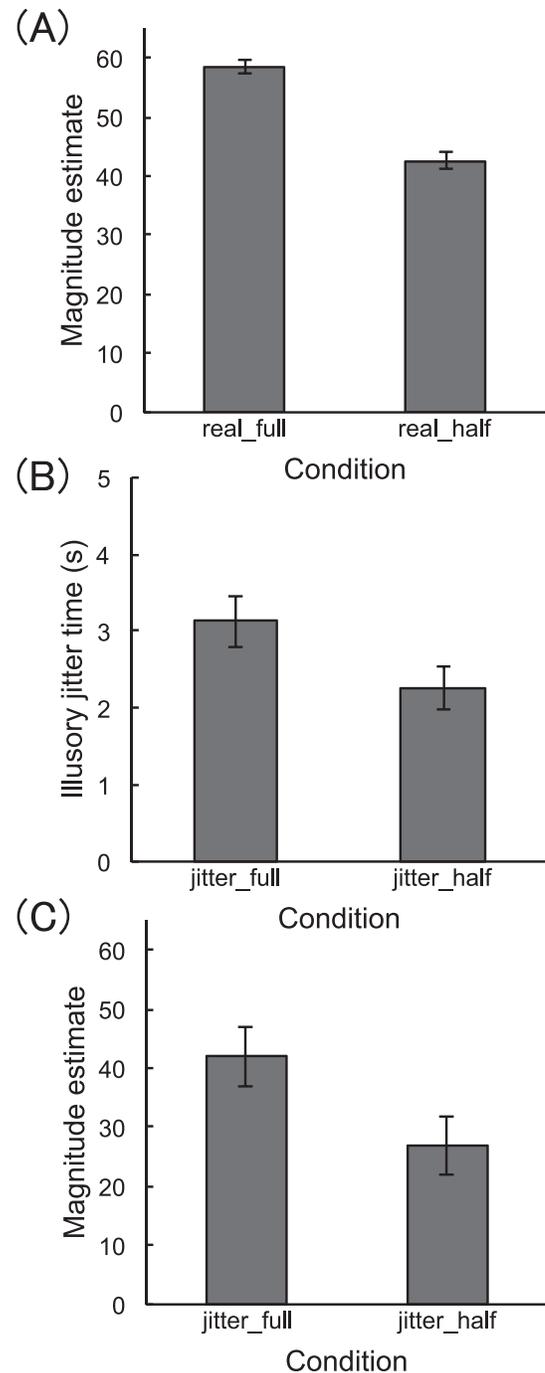

Figure 3. Motion strength as measured by timing and magnitude estimation. Error bars indicate ±1 *SE*. (A) Averaged magnitude estimate for the real oscillation; (B) averaged time data indicating how long the illusory jitter persisted when observation was unlimited in time; (C) averaged magnitude estimate for the illusory jitter.

condition (Figure 2). A one-way repeated-measures analysis of variance (ANOVA) confirmed a significant main effect of condition, $F(4, 40) = 17.65$, $p < 0.0001$. The ANOVA was followed by multiple comparisons using Shaffer's modified sequentially rejective Bonfer-
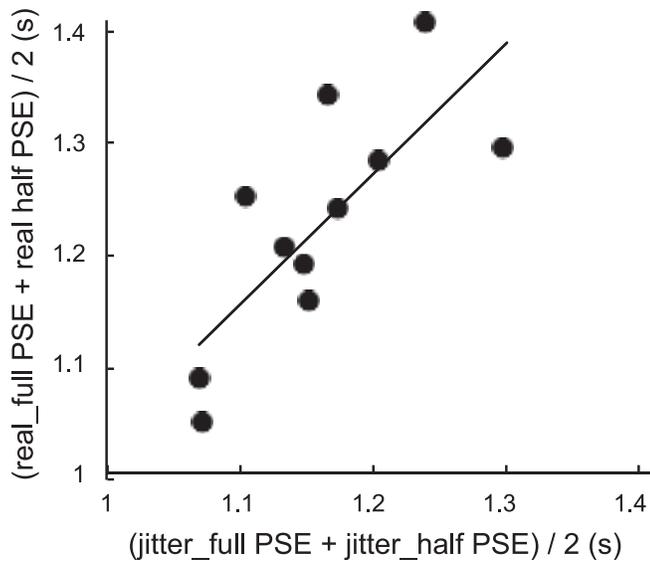
Figure 4. Interobserver scattergram visualizing a correlation between the subjective durations for the illusory jitter and the real oscillation. The line indicates the best-fit linear regression model.

roni procedure; they revealed that, compared with the *baseline* PSE, the PSE data differed significantly under the *real_full*, $t(10) = 6.75$, adjusted $p < 0.0005$, and *real_half*, $t(10) = 7.74$, adjusted $p < 0.0005$, conditions. However, they did not differ significantly from each other, $t(10) = 0.76$, adjusted $p = 0.93$.

Therefore, time dilation occurred when a stimulus actually oscillated on the display to mimic what was perceived in the jitter aftereffect. Remarkably, time dilation was as vigorous even at 1.5 min oscillation amplitude (i.e., *real_half*). The fraction of overestimation was 16%–17% of the *baseline* PSE.

Illusory jitter

Did a similar time dilation occur when a stimulus was actually static on the display but subjective motion was experienced as a similar random oscillation? To produce the jitter aftereffect, we presented a dynamic random-dot pattern in the surrounding region during the adaptation period that lasted for 10 s in the *jitter_full* condition and 5 s in the *jitter_half* condition. To check that the jitter aftereffect occurred as intended, in a separate experiment, we asked observers to time illusory jitter in the test period, during which both the central and surrounding dot patterns remained static on the display until the observer pressed a key. Under the *jitter_full* condition, illusory jitter lasted for 3.13 ± 0.34 s, which was significantly greater than 1.2 s (two-tailed *t* test), $t(10) = 5.74$, $p < 0.0005$, the duration of the test stimulus used in the main experiment (Figure 3B). Under the *jitter_half* condition, illusory jitter

lasted for 2.25 ± 0.27 s, again significantly greater than 1.2 s, $t(10) = 3.87$, $p < 0.005$. A significant difference was also found between these conditions (two-tailed paired *t* test), $t(10) = 4.37$, $p < 0.005$. Furthermore, the magnitude estimates under the *jitter_full* (41.9 ± 5.0) and *jitter_half* (26.7 ± 5.0) conditions differed significantly from each other, $t(10) = 5.71$, $p < 0.0005$ (Figure 3C).

The PSE data under the *jitter_full* and *jitter_half* conditions were greater than under the *baseline* condition (Figure 2). The ANOVA and subsequent multiple comparisons revealed that, compared with the *baseline* PSE, the PSE data differed significantly under the *jitter_full*, $t(10) = 3.84$, adjusted $p < 0.05$, and *jitter_half*, $t(10) = 6.60$, adjusted $p < 0.0005$, conditions. However, they did not differ significantly from each other, $t(10) = 0.19$, adjusted $p = 0.93$.

These results unequivocally demonstrate time dilation in an actually static but perceptually moving visual pattern. The fraction of overestimation was approximately 10% of the *baseline* PSE.

Correlation between the time dilations for illusory and real motions

When individual data were considered, there seemed to be a pattern of similarities between the PSE data in the illusory jitter and in the real oscillation. To visualize this relationship, an interobserver scattergram was plotted with the average of the *jitter_full* and *jitter_half* PSE data on the abscissa and the average of the *real_full* and *real_half* PSE data on the ordinate (Figure 4). The correlation coefficient was significantly positive, Pearson's $r = .76$, $t(9) = 3.56$, $p < 0.01$, indicating that observers who experienced a greater time dilation in the illusory jitter tended to experience a greater dilation in the real oscillation as well. This relationship was not due to the individual variability in baseline performance because the correlation was still significantly positive even if the PSE data were expressed as a fraction of the *baseline* PSE for each observer, $r = .61$, $t(9) = 2.28$, $p < 0.05$.

The result of a paired *t* test between the horizontal and vertical data was significant, $t(10) = 3.08$, $p < 0.05$, and linear regression analysis yielded the best-fit model $y = 1.16 \ x − .13$ ($R^2 = .58$), indicating that the jitter aftereffect was less effective than the real oscillation in evoking time dilation but that the difference between them was only modest.

Slope

The cumulative Gaussian psychometric function's σ differed significantly across conditions (one-way re-
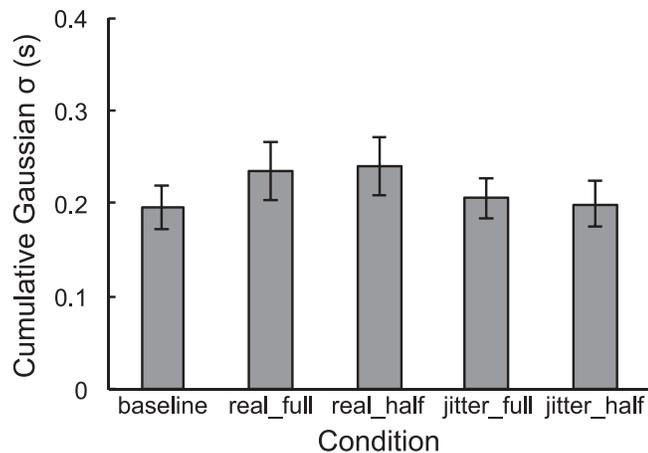
Figure 5. Averaged standard deviation (σ) plotted against condition. The upward direction of the ordinate indicates shallower slope. Error bars indicate ±1 SE.

peated-measures ANOVA), $F(4, 40) = 3.54$, $p < 0.05$, although no condition pairs survived multiple comparisons (Figure 5). If illusory jitter's perceived motion strength or its impact on duration perception had fluctuated from trial to trial, a shallower slope would have been predicted in the *jitter_full* and *jitter_half* conditions; on the contrary, the slopes under these conditions were virtually identical to that under the baseline condition and apparently steeper than under the real oscillation conditions. Therefore, these results confirmed the robustness of the jitter aftereffect. Because we used the same set of comparison stimuli across conditions, the seemingly larger σs under the *real_full* and *real_half* conditions should have stemmed from noisier observation of the actually oscillating test stimulus. Possible noise processes may include external noises inherent in the stochastic nature of the actual image oscillation and internal noises such as trial-by-trial fluctuation in neural activations driven by the actual image motion.

Discussion

To summarize the results, (a) a random-dot pattern moving in random oscillations as tiny as retinal image motions due to fixational eye movements appeared to last longer than a stationary stimulus, (b) time dilation occurred even when oscillations were illusory, (c) the observers who experienced a greater time dilation in an actually oscillating stimulus also did so in an only subjectively jittering pattern, and (d) time dilation did not significantly vary with the strength of the jitter aftereffect or with the amplitude of the real oscillation. These findings clearly indicate the involvement of complex motion processing prior to determination of

perceived duration. What kind of complex motion processing is specifically considered as influencing duration representation? According to Murakami and Cavanagh (1998), the visual system normally prevents retinal image motions due to small eye movements from appearing as an oscillating visual world, but such a compensatory mechanism is impaired for some time after adaptation to dynamic noise. The visual system makes a mistake of emphasizing jittery image motions in the unadapted region in reference to the adapted region, where fatigued motion sensors have become less sensitive to image motion signals even though incessant fixational eye movements physically yield jittery image motions in the same way in the adapted and unadapted regions. Such a referenced motion may be picked up by neurons with center-surround antagonism with respect to motion direction, and such a receptive field property has been found in area MT/V5 and its downstream (Allman, Miezin, & McGuinness, 1985; Eifuku & Wurtz, 1998; Komatsu & Wurtz, 1988; Lagae, Gulyas, Raiguel, & Orban, 1989; Tanaka et al., 1986; Tanaka, Sugita, Moriya, & Saito, 1993). Consistent with this theory, the human MT+ is activated during perception of the jitter aftereffect (Y. Sasaki, Murakami, Cavanagh, & Tootell, 2002). Thus, this study suggests that the duration perception quantified here is mediated by some processing stage receiving inputs from a high-level motion computation process used to establish a stable visual world despite fixational eye movements and that a neurophysiological candidate for such a stage resides in area MT/V5 or higher.

Time dilation was robustly observed in a pattern in tiny oscillation for both the actual image oscillation and mere phenomenal jitter (Figure 2). Additionally, only 1.5–3 min oscillation amplitude, which is close to the resolution acuity, was sufficient. This is worth reporting by itself because previous studies have usually used widely traveling or drifting stimuli to induce time dilation. At first glance, this finding might seem at odds with previous investigations indicating that more vigorous motion yields greater time dilation. However, the temporal frequency of 7.5 Hz of our actually oscillating stimuli was well within the range of motion stimuli for which time dilation has previously been reported (Kanai et al., 2006). The point is that back-and-forth movements in a very tiny excursion can be an effective stimulus given that the movements are sufficiently rapid.

There was a positive interobserver correlation between the results for the illusory jitter and for the real oscillation (Figure 4). This relationship suggests not only that they share a common mechanism but also that such a common mechanism feeds into a common duration computation process, affecting duration perception in a similar fashion. If that is the case, parsimony dictates that the actually oscillating stimulus alters duration

perception via the very pathway used to produce the jitter aftereffect, which arguably requires high-level motion processing according to the above discussion.

We tested stronger and weaker motions for both the illusory jitter and the real oscillations and confirmed their perceptual discriminability, but we failed to obtain clear differences in the amount of time dilation. Nevertheless, it is remarkable that even the weakest of the tested motions still yielded almost equally robust time dilation compared with the other motion conditions. Whether such a robust dilation occurs in motion at absolute threshold or even weaker remains an outstanding question.

The occurrence of time dilation in an actually static but subjectively jittering pattern is compatible with several theories for duration computation. One of the most influential models, called the pacemaker–accumulator model, assumes an internal pacemaker that ticks counts in subsecond resolution, an accumulator that accumulates the tick counts within a time period demarcated by signals of stimulus onset and offset, and a comparator that compares the accumulated data with stored templates modeling a variety of durations (Grondin, 2010). A computational state subjectively experienced as motion perception may affect the behavior of the pacemaker–accumulator network, perhaps by increasing the tick rate of the pacemaker or by decreasing the lapse rate of the accumulator, in comparison with the state from which no motion perception is evoked. Additionally, the present findings are explainable by the model of energy expenditure in the dorsal pathway (Eagleman & Pariyadath, 2009); according to this theory, a stimulus appears to last longer as a larger neurophysiological cost is required to bring it up to one's consciousness. If motion computation to estimate the motion in the central region in reference to the fatigued surround imposes additional neural cost in the jitter aftereffect, the perception of it would accompany greater energy expenditure, probably in the dorsal pathway where spatial contrasting of visual motion signals is one of the major tasks. A recent study suggested that a static figure implying object movement may appear to last slightly longer than a static figure unrelated to movement (Yamamoto & Miura, 2012b), and such implied motion was reported to activate the human MT+ (Kourtzi & Kanwisher, 2000; Williams & Wright, 2009; but see Lorteije et al., 2011). In such a case, it might be that time appears to dilate more or less whenever a visual scene is consciously interpreted to have movement in general as a result of motion computation in the dorsal pathway. In addition, the present findings might be consistent with another currently popular model called the striatal beat-frequency model, which emphasizes a snapshot of population activities of oscillatory neurons as a signature of a specific duration. Recently, this model was extended to account for time dilation in light stimuli containing alpha-band flicker frequencies by incorporating a neural plasticity that oscillation frequencies can be entrained by outer rapid events (Hashimoto & Yotsumoto, 2015). Our results could be explained if the neural correlates of the jitter aftereffect and real oscillation exert a similar entraining function to the beat-frequency network, but a precise form of implementation requires future empirical data and simulations.

Our findings are orthogonal to some other explanation principles, however. For example, it is unlikely that attention/arousal played a major role because our observers must have been equally vigilant and attentive to the stimuli in performing the duration comparison task; the slopes of the psychometric functions did not systematically differ depending on conditions. Additionally, our findings cannot be explained by the plasticity in temporal impulse response of magnocellular LGN neurons as neural registers of time flow because feed-forward registration of retinal image motions must have been done in equal fashion whether the actually static pattern subjectively appeared as static or jittering. Nevertheless, the attention/arousal and LGN activation are still viable hypotheses for duration perception in general and are not necessarily in conflict with this study. It would be interesting to examine whether attention/arousal can add further time dilation to that presently observed if a subjective oscillation suddenly appears as an oddball as well as whether time dilation in illusory jitter survives in band-limited stimulation to escape activation of a certain population of early visual cells.

Conclusions

To sum up, illusory jitter in a static image as well as real image oscillation appeared to last longer, and rapid oscillatory motion as tiny as the resolution acuity limit robustly produced this time illusion. These findings indicate that stimulus motion is not requisite for time dilation to occur; conscious experience of motion is the essential determinant factor. Therefore, high-level motion processing mediating such experiences also conceivably mediates duration computation around a second.

Keywords: duration, motion, illusion, aftereffect, time perception

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References

Allman, J., Miezin, F., & McGuinness, E. (1985). Direction-and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area (MT). *Perception, 14*, 105–126, doi:10.1068/p140105.

Au, R. K. C., Ono, F., & Watanabe, K. (2012). Time dilation induced by object motion is based on spatiotopic but not retinotopic positions. *Frontiers in Psychology, 3*(58), 1–7, doi:10.3389/fpsyg.2012.00058.

Ayhan, I., Bruno, A., Nishida, S., & Johnston, A. (2009). The spatial tuning of adaptation-based time compression. *Journal of Vision, 9*(11):2, 1–12, doi:10.1167/9.11.2. [PubMed] [Article]

Ayhan, I., Bruno, A., Nishida, S., & Johnston, A. (2011). Effect of the luminance signal on adaptation-based time compression. *Journal of Vision, 11*(7):22, 1–17, doi:10.1167/11.7.22. [PubMed] [Article]

Binetti, N., Lecce, F., & Doricchi, F. (2012). Time-dilation and time-contraction in an anisochronous and anisometric visual scenery. *Journal of Vision, 12*(7):8, 1–19, doi:10.1167/12.7.8. [PubMed] [Article]

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10*(4), 433–436, doi:10.1163/156856897X00357.

Brown, S. W. (1995). Time, change, and motion: The effects of stimulus movement on temporal perception. *Perception & Psychophysics, 57*(1), 105–116, doi:10.3758/BF03211853.

Bruno, A., Ayhan, I., & Johnston, A. (2010). Retinotopic adaptation-based visual duration compression. *Journal of Vision, 10*(10):30, 1–18, doi:10.1167/10.10.30. [PubMed] [Article]

Bruno, A., Ayhan, I., & Johnston, A. (2012). Effects of temporal features and order on the apparent duration of a visual stimulus. *Frontiers in Psychology, 3*(90), 1–7, doi:10.3389/fpsyg.2012.00090.

Burr, D., Cicchini, G., Arrighi, R., & Morrone, M. (2011). Spatiotopic selectivity of adaptation-based compression of event duration. *Journal of Vision, 11*(2):21, 1–9, doi:10.1167/11.2.21. [PubMed] [Article]

Burr, D., Tozzi, A., & Morrone, M. C. (2007). Neural mechanisms for timing visual events are spatially selective in real-world coordinates. *Nature Neuroscience, 10*(4), 423–425, doi:10.1038/nn1874.

Casini, L., & Macar, F. (1997). Effects of attention manipulation on judgments of duration and of intensity in the visual modality. *Memory & Cognition, 25*(6), 812–818, doi:10.3758/BF03211325.

Cicchini, G. M., & Morrone, M. C. (2009). Shifts in spatial attention affect the perceived duration of events. *Journal of Vision, 9*(1):9, 1–13, doi:10.1167/9.1.9. [PubMed] [Article]

Curran, W., & Benton, C. P. (2012). The many directions of time. *Cognition, 122*(2), 252–257, doi:10.1016/j.cognition.2011.10.016.

Eagleman, D. M., & Pariyadath, V. (2009). Is subjective duration a signature of coding efficiency? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 364*(1525), 1841–1851, doi:10.1098/rstb.2009.0026.

Eifuku, S., & Wurtz, R. H. (1998). Response to motion in extrastriate area MSTl: Center-surround interactions. *Journal of Neurophysiology, 80*(1), 282–296.

Gorea, A., & Kim, J. (2015). Time dilates more with apparent than with physical speed. *Journal of Vision, 15*(1):7, 1–11, doi:10.1167/15.1.7. [PubMed] [Article]

Grondin, S. (2010). Timing and time perception: A review of recent behavioral and neuroscience findings and theoretical directions. *Attention, Perception, & Psychophysics, 72*(3), 561–582, doi:10.3758/APP.72.3.561.

Hashimoto, Y., & Yotsumoto, Y. (2015). Effect of temporal frequency spectra of flicker on time perception: Behavioral testing and simulations using a striatal beat frequency model. *Timing & Time Perception, 3*, 201–222.

Hellström, Å. (1979). Time errors and differential sensation weighting. *Journal of Experimental Psychology: Human Perception and Performance, 5*(3), 460–477, doi:10.1037/0096-1523.5.3.460.

Hellström, Å. (2003). Comparison is not just subtraction: Effects of time- and space-order on subjective stimulus difference. *Perception & Psychophysics, 65*(7), 1161–1177, doi:10.3758/BF03194842.

Hellström, Å. (1985). The time-order error and its

relatives: Mirrors of cognitive processes in comparing. *Psychological Bulletin, 97*(1), 35–61, doi:10.1037/0033-2909.97.1.35.

Herbst, S. K., van der Meer, E., & Busch, N. A. (2012). Attentional selection dilates perceived duration. *Perception, 41*(8), 883–900, doi:10.1068/p7300.

Johnston, A., Arnold, D. H., & Nishida, S. (2006). Spatially localized distortions of event time. *Current Biology, 16*(5), 472–479, doi:10.1016/j.cub.2006.01.032.

Johnston, A., Bruno, A., & Ayhan, I. (2011). Retinotopic selectivity of adaptation-based compression of event duration: Reply to Burr, Cicchini, Arrighi, and Morrone. *Journal of Vision, 11*(2):21a, 1–3, doi:10.1167/11.2.21a. [Article]

Johnston, A., Bruno, A., Watanabe, J., Quansah, B., Patel, N., Dakin, S., & Nishida, S. (2008). Visually-based temporal distortion in dyslexia. *Vision Research, 48*(17), 1852–1858, doi:10.1016/j.visres.2008.04.029.

Kanai, R., Paffen, C. L. E., Hogendoorn, H., & Verstraten, F. A. J. (2006). Time dilation in dynamic visual display. *Journal of Vision, 6*(12):8, 1421–1430, doi:10.1167/6.12.8. [PubMed] [Article]

Kanai, R., & Watanabe, M. (2006). Visual onset expands subjective time. *Perception & Psychophysics, 68*(7), 1113–1123, doi:10.3758/BF03193714.

Kaneko, S., & Murakami, I. (2009). Perceived duration of visual motion increases with speed. *Journal of Vision, 9*(7):14, 1–12, doi:10.1167/9.7.14. [PubMed] [Article]

Kleiner, M., Brainard, D. H., & Pelli, D. (2007). What's new in Psychtoolbox-3? *Perception, 36*(1 Suppl.), 14, doi:10.1068/v070821.

Komatsu, H., & Wurtz, R. H. (1988). Relation of cortical areas MT and MST to pursuit eye movements. III. Interaction with full-field visual stimulation. *Journal of Neurophysiology, 60*(2), 621–644.

Kourtzi, Z., & Kanwisher, N. (2000). Activation in human MT/MST by static images with implied motion. *Journal of Cognitive Neuroscience, 12*(1), 48–55, doi:10.1162/08989290051137594.

Lagae, L., Gulyas, B., Raiguel, S., & Orban, G. A. (1989). Laminar analysis of motion information processing in macaque V5. *Brain Research, 496*(1–2), 361–367, doi:10.1016/0006-8993(89)91089-5.

Lejeune, H. (1998). Switching or gating? The attentional challenge in cognitive models of psychological time. *Behavioural Processes, 44*(2), 127–145, doi:10.1016/S0376-6357(98)00045-X.

Linares, D., & Gorea, A. (2015, Mar 6). Temporal

frequency of events rather than speed dilates perceived duration of moving objects. *Scientific Reports, 5*(8825), 1–9, doi:10.1038/srep08825.

Lorteije, J. A., Barraclough, N. E., Jellema, T., Raemaekers, M., Duijnhouwer, J., Xiao, D., . . . van Wezel, R. J. (2011). Implied motion activation in cortical area MT can be explained by visual low-level features. *Journal of Cognitive Neuroscience, 23*(6), 1533–1548, doi:10.1162/jocn.2010.21533.

Matthews, W. J. (2011). How do changes in speed affect the perception of duration? *Journal of Experimental Psychology: Human Perception and Performance, 37*(5), 1617–1627, doi:10.1037/a0022193.

Murakami, I., & Cavanagh, P. (1998, Oct 22). A jitter after-effect reveals motion-based stabilization of vision. *Nature, 395*(6704), 798–801, doi:10.1038/27435.

Murakami, I., & Cavanagh, P. (2001). Visual jitter: Evidence for visual-motion-based compensation of retinal slip due to small eye movements. *Vision Research, 41*(2), 173–186, doi:10.1016/S0042-6989(00)00237-6.

Ono, F., & Kawahara, J.-I. (2007). The subjective size of visual stimuli affects the perceived duration of their presentation. *Perception & Psychophysics, 69*(6), 952–957, doi:10.3758/BF03193932.

Ono, F., & Kitazawa, S. (2009). The effect of marker size on the perception of an empty interval. *Psychonomic Bulletin & Review, 16*(1), 182–189, doi:10.3758/PBR.16.1.182.

Pariyadath, V., & Eagleman, D. (2007). The effect of predictability on subjective duration. *PloS One, 2*(11), e1264, doi:10.1371/journal.pone.0001264.

Pariyadath, V., & Eagleman, D. M. (2008). Brief subjective durations contract with repetition. *Journal of Vision, 8*(8):16, 1–6, doi:10.1167/8.16.11. [PubMed] [Article]

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10*(4), 437–442, doi:10.1163/156856897X00366.

Perrone, J. A., & Thiele, A. (2002). A model of speed tuning in MT neurons. *Vision Research, 42*(8), 1035–1051, doi:10.1016/S0042-6989(02)00029-9.

Priebe, N. J., Cassanello, C. R., & Lisberger, S. G. (2003). The neural representation of speed in macaque area MT/V5. *Journal of Neuroscience, 23*(13), 5650–5661.

Priebe, N. J., & Lisberger, S. G. (2004). Estimating target speed from the population response in visual

area MT. *Journal of Neuroscience, 24*(8), 1907–1916, doi:10.1523/JNEUROSCI.4233-03.2004.

Prins, N. (2012). The psychometric function: The lapse rate revisited. *Journal of Vision, 12*(6):25, 1–16, doi:10.1167/12.6.25. [PubMed] [Article]

Prins, N., & Kingdom, F. A. A. (2009). *Palamedes: Matlab routines for analyzing psychophysical data.* Retrieved from http://www.palamedestoolbox.org

Rammsayer, T. H., & Verner, M. (2014). The effect of nontemporal stimulus size on perceived duration as assessed by the method of reproduction. *Journal of Vision, 14*(5):17, 1–10, doi:10.1167/14.5.17. [PubMed] [Article]

Roelofs, C. O., & Zeeman, W. P. C. (1951). Influence of different sequences of optical stimuli on the estimation of duration of a given interval of time. *Acta Psychologica, 8*, 89–128, doi:10.1016/0001-6918(51)90007-8.

Sasaki, K., Yamamoto, K., & Miura, K. (2013). The difference in speed sequence influences perceived duration. *Perception, 42*(2), 198–207, doi:10.1068/p7241.

Sasaki, Y., Murakami, I., Cavanagh, P., & Tootell, R. H. B. (2002). Human brain activity during illusory visual jitter as revealed by functional magnetic resonance imaging. *Neuron, 35*(6), 1147–1156, doi:10.1016/S0896-6273(02)00899-1.

Schindel, R., Rowlands, J., & Arnold, D. H. (2011). The oddball effect: Perceived duration and predictive coding. *Journal of Vision, 11*(2):17, 1–9, doi:10.1167/11.2.17. [PubMed] [Article]

Seifried, T., & Ulrich, R. (2011). Exogenous visual attention prolongs perceived duration. *Attention, Perception & Psychophysics, 73*, 68–85, doi:10.3758/s13414-010-0005-6.

Stetson, C., Fiesta, M. P., & Eagleman, D. M. (2007). Does time really slow down during a frightening event? *PloS One, 2*(12), e1295, doi:10.1371/journal.pone.0001295.

Takemura, H., & Murakami, I. (2010). Visual motion detection sensitivity is enhanced by orthogonal induced motion. *Journal of Vision, 10*(2):9, 1–13, doi:10.1167/10.2.9. [PubMed] [Article]

Tanaka, K., Hikosaka, K., Saito, H., Yukie, M.,

Fukada, Y., & Iwai, E. (1986). Analysis of local and wide-field movements in the superior temporal visual areas of the macaque monkey. *Journal of Neuroscience, 6*(1), 134–144.

Tanaka, K., Sugita, Y., Moriya, M., & Saito, H. (1993). Analysis of object motion in the ventral part of the medial superior temporal area of the macaque visual cortex. *Journal of Neurophysiology, 69*(1), 128–142.

Tse, P. U., Intriligator, J., Rivest, J., & Cavanagh, P. (2004). Attention and the subjective expansion of time. *Perception & Psychophysics, 66*(7), 1171–1189, doi:10.3758/BF03196844.

Ulrich, R., Nitschke, J., & Rammsayer, T. (2006). Perceived duration of expected and unexpected stimuli. *Psychological Research, 70*(2), 77–87, doi:10.1007/s00426-004-0195-4.

Vicario, C. M., Pecoraro, P., Turriziani, P., Koch, G., Caltagirone, C., & Oliveri, M. (2008). Relativistic compression and expansion of experiential time in the left and right space. *PLoS ONE, 3*(3), e1716, doi:10.1371/journal.pone.0001716.

Wang, L., & Jiang, Y. (2012). Life motion signals lengthen perceived temporal duration. *Proceedings of the National Academy of Sciences, USA, 109*(11), E673–E677, doi:10.1073/pnas.1115515109.

Williams, A. L., & Wright, M. J. (2009). Static representations of speed and their neural correlates in human area MT/V5. *Neuroreport, 20*(16), 1466–1470, doi:10.1097/WNR.0b013e32833203c1.

Yamamoto, K. (2016). Effect of motion coherence on time perception relates to perceived speed. *Vision Research, 123*, 56–62, doi:10.1016/j.visres.2015.11.004.

Yamamoto, K., & Miura, K. (2012a). Perceived duration of plaid motion increases with pattern speed rather than component speed. *Journal of Vision, 12*(4):1, 1–13, doi:10.1167/12.4.1. [PubMed] [Article]

Yamamoto, K., & Miura, K. (2012b). Time dilation caused by static images with implied motion. *Experimental Brain Research, 223*(2), 311–319, doi:10.1007/s00221-012-3259-5.