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Non-uniform transformation of subjective time during action preparation

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Abstract

Although many studies have reported a distortion of subjective (internal) time during preparation and execution of actions, it is highly controversial whether actions cause a dilation or compression of time. In the present study, we tested a hypothesis that the previous controversy (dilation vs. compression) partly resulted from a mixture of two types of sensory inputs on which a time length was estimated; some studies asked subjects to measure the time of presentation for a single continuous stimulus (stimulus period, e.g. the duration of a long-lasting visual stimulus on a monitor) while others required estimation of a period without continuous stimulations (no-stimulus period, e.g. an inter-stimulus interval between two flashes). Results of our five experiments supported this hypothesis, showing that action preparation induced a dilation of a stimulus period, whereas a no-stimulus period was not subject to this dilation and sometimes can be compressed by action preparation. Those results provided a new insight into a previous view assuming a uniform dilation or compression of subjective time by actions. Our findings about the distinction between stimulus and no-stimulus periods also might contribute to a resolution of mixed results (action-induced dilation vs. compression) in a previous literature.

Key words: internal clock; motor commands; time representation; gap detection

1.Introduction

Sensation of time is an essential ability for humans (Matell & Meck, 2004; Nobre & O'Reilly, 2004). Accurate estimation of the duration of a stimulus and an inter-stimulus interval (ISI) is necessary when we understand someone’s speech and listen to music (Macar et al., 2002; Mauk & Buonomano, 2004). Time sensation also plays a critical role in a coordination of complex and rhythmic movements such as walking and dancing (Lewis & Miall, 2003). Despite this importance, our sensations and representations of time (subjective time) are not always accurate but influenced by various psychological factors, such as attention (Macar, Grondin, & Casini, 1994) and emotion (Droit-Volet & Meck, 2007). Of particular interest in these days is a distortion of time induced by an execution and observation of actions (Desantis, Waszak, Moutsopoulou, & Haggard, 2016; Haggard, Clark, & Kalogeras, 2002; Press & Cook, 2015; Watanabe, 2008; Yarrow, Haggard, Heal, Brown, & Rothwell, 2001).

This distortion of time can be typically seen when sensory stimuli are presented around the moment of actions. Some studies showed that subjective time for a visual event before (Hagura, Kanai, Orgs, & Haggard, 2012) and after (Park, Schlag-Rey, & Schlag, 2003) a voluntary manual movement was overestimated compared to actual duration of that event (action-related dilation of time). In contrast, others (Binda, Cicchini, Burr, & Morrone, 2009; Morrone, Ross, & Burr, 2005; Yokosaka, Kuroki, Nishida, & Watanabe, 2015) reported an underestimation of an interval between two visual stimuli at the time of hand movements and saccades (action-related compression of time). This inconsistency among researches (dilation vs. compression) is seen not only on visual but also on somatosensory stimuli. A recent study (Press, Berlot, Bird, Ivry, & Cook, 2014) reported that the vibrations applied to a moving finger were perceived to be longer than those to a stationary finger (dilation), while another (Tomassini, Gori, Baud-Bovy, Sandini, & Morrone, 2014) showed that an perceived interval between tactile taps was shorter when those taps were presented to moving than static hands (compression). Overall, there has been no unified view as to whether actions induce a dilation or compression of subjective time.

How can we resolve this inconsistency? One way is to examine differences in experimental designs and parameters among previous studies, thereby identifying critical factor(s) producing the mixed results. First possible factor would be a relative timing of stimuli to actions. In one study, target stimuli for estimation of time were presented before an execution of actions (Hagura et al., 2012). In other words, they measured time sensations *before* action execution (pre-action design). Many other studies, however, did not use the pre-action design, giving target stimuli *during* (Yokosaka et al., 2015), *after* (Park et al., 2003), or around (Morrone et al., 2005; Press et al., 2014; Tomassini et al., 2014) the moment of actions. Since an action is a complex process involving a sequence of multiple stages (preparation, execution, and termination, etc.), this variability in relative timings of stimuli to actions (before, during, or after) might cause the mixed results in a previous literature. Another possible factor for the inconsistency would be differences in types of actions (motor effectors) in previous studies. One study reported an action-related compression of time induced by saccadic eye movements (Morrone et al., 2005), while others showed a time dilation by manual movements, such as reaching (Hagura et al., 2012), finger lifting (Press et al., 2014), and key pressing (Park et al., 2003). It might be thus possible that movements of eyes and hands induce compression and dilation of time, respectively. Recent studies, however, reported evidence against this view (time compression by hand movements (Tomassini et al., 2014; Tomassini & Morrone, 2016; Yokosaka et al., 2015)).

Those differences among previous studies suggest several factors affecting a direction (dilation vs. compression) of action-related distortion of time. In the present study, we focused on a new parameter that has received little attention so far; the presence of continuous inputs during a period to be estimated. In some studies, subjects measured the *duration* of a single continuous stimulus (stimulus period). The action-related dilation was reported in all those studies (Hagura et al., 2012; Park et al., 2003; Press et al., 2014). In another group of studies, subjects estimated an *interval* between two brief stimuli (ISI, no-stimulus period), most of which reported the action-related compression (Morrone et al., 2005; Tomassini et al., 2014; Yokosaka et al., 2015). Those results suggest that the presence/absence of continuous inputs (duration vs. ISI) might be a key factor modulating a direction and a magnitude of time distortion.

2. Experiment 1

Based on an idea above, we first compared action-related time distortions under two conditions (**Fig. 1**). In one condition, subjects viewed a single continuous stimulus (a white disk of 950 - 1450 ms), performing key-pressing movements as soon as it disappeared from a screen. They then judged the duration of the white disk by comparing it with a reference stimulus (1200 ms) presented after the key-pressing movements (duration condition, **Fig. 1A**). In another condition (interval condition, **Fig. 1B**), one trial involved four brief (17 ms) flashes of a white disk, two in a pre-action period and two in a post-action period. After performing the key-press actions to the 2nd flash, subjects compared an ISI between the 1st and 2nd flashes (950 – 1450 ms) with that between the 3rd and 4th flashes (1200 ms). If the factor we assumed above (the presence/absence of continuous inputs) is critical, those two conditions (duration vs. interval) would produce different patterns of time distortions induced by the same actions.

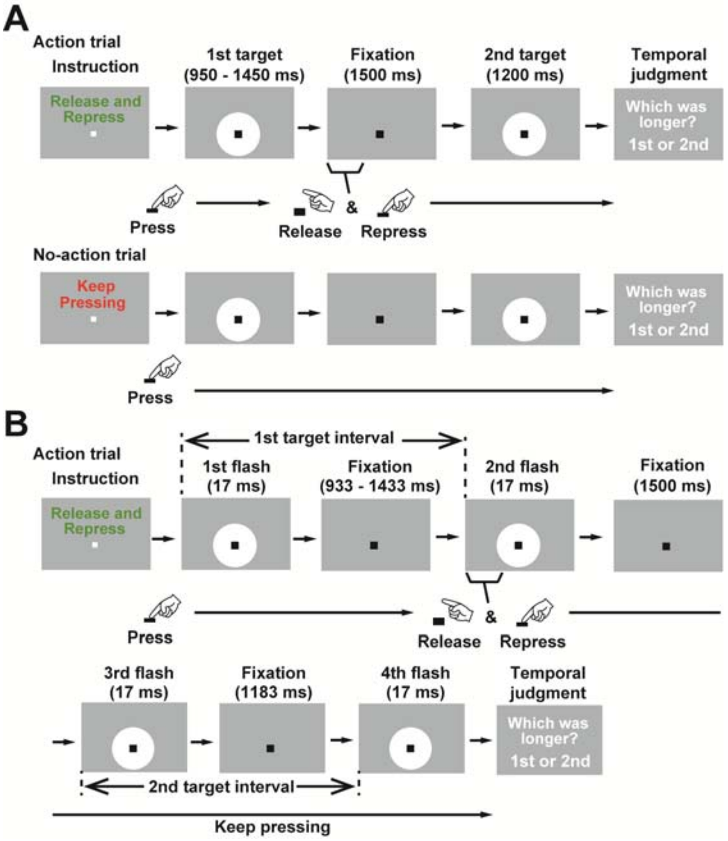

Figure 1. Structures of trials in Experiment 1. (**A**) Duration condition. Subjects started each trial by pressing a key after reading an instruction message ("Release and Repress" or "Keep Pressing") on a screen. In action trials (upper panels), they released and repressed the key as soon as a white disk (1st target) disappeared from the screen. They then viewed the 2nd target while pressing the key and judged whether the 1st or 2nd target was presented longer (temporal judgment task). The lower panels illustrate a control (no-action) trials in which subject performed no actions but kept pressing a key until a screen for the temporal judgment task was presented. An influence of action preparation on time perception was measured by comparing subjective duration of the 1st target between the action and no-action trials. (**B**) Interval condition. One trial involved four flashes of a white disk. Subjects compared an interval (stimulus onset asynchrony) between the 1st and 2nd flashes (1st target) with that between the 3rd and 4th flashes (2nd target). They performed the release and repress movement in response to the 2nd flash (action trials) while no action was necessary in control

(no-action) trials (not shown in this figure).

As shown in **Figure 1**, we presently used the pre-action design in which target stimuli for time estimation were presented before actions. This was based on the following two reasons. First, Hagura et al. (2012) used the pre-action design and showed an action-related dilation of visual events induced by manual movements. Importantly, they demonstrated this effect by excluding contributions of any non-action factors, such as attention and an elevation of arousal level accompanying action preparation. Furthermore, their results (action-related dilation) were supported not only by a subjective measure (a perceived length of time) but also by objective measures such as detection rates of rapidly-presented visual stimuli. Those solid results acquired through the pre-action design would provide a firm basis to test an effect of stimulus continuity (duration vs. ISI) in the present study. Second, the pre-action design can avoid a possible influence of somatosensory inputs caused by action execution. Since time estimation for the 1st target (duration or ISI, **Fig. 1**) was made before action execution, it was unlikely in the present study that peripheral sensor changes induced by action execution affected a subjective length of the target (pre-action) stimuli. Any effect on subjective duration (or ISI) can be thus attributed to the central processing (action preparation), which would make it easy to interpret the present data.

2.1. Methods

2.1.1. Subjects

Eighteen subjects participated in Experiment 1. This number of participants per experiment is equivalent to or larger than previous studies investigating an effect of actions on time sensation (Hagura et al., 2012; Press et al., 2014; Tomassini et al., 2014; Yokosaka et al., 2015). Most of those subjects were collected through a recruitment system in Kobe University, Japan. All had normal or corrected-to-normal vision. Informed consent was received from each subject after the nature of the study had been explained. All experiments were carried out in accordance with guidelines and regulations approved by the ethics committee of Kobe University.

2.1.2. Stimuli and task

All visual stimuli were generated using the MATLAB Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and presented on a CRT monitor (resolution: 1024 × 768 pixels) at a refresh rate of 60 Hz. In the duration condition (**Fig. 1A**), each trial started with an instruction screen indicating key-press actions required in that trial. A message on the instruction screen was "Release and Repress" (action trial) or "Keep Pressing" (no-action trial), and it was placed at a position slightly above a white fixation point (0.19 × 0.19 deg) on a gray background. When subjects read the message and pressed a key with their right hand, the message went off and a color of the fixation changed into black. After a random delay of 1000 – 1900 ms (during which subjects kept pressing the key), a white disk (1st target, 3.13 × 3.13 deg) appeared over the fixation for 950, 1050, 1150, 1250, 1350, or 1450 ms (variable across trials), which was followed by a fixation-only screen for 1500 ms. In the action trials ("Release and Repress"), subjects had to release the key when the 1st target went off, and press it again. Importantly, both of those "release" and "repress" actions should be performed as quickly as possible, within 500 ms from an offset of the 1st target. Otherwise, they saw an error message informing an abortion of a current trial (the aborted trial was repeated later in the same experimental session). In the no-action trials ("Keep Pressing"), on the other hand, subjects had to keep pressing the key even after an offset of the 1st target (an error message was shown when they released the key). Subjects then saw the 2nd target (white disk) presented at the same position as the 1st target (note that the key was being pressed both in the action and no-action trials during this 2nd-target period). The duration of the 2nd target was 1200 ms in every trial, although this information was unknown to subjects. Finally, a task screen was presented on the screen that allowed subjects to release the key and prompted them to perform a temporal judgment task. In this task, subjects compared the duration of the 1st target (950 – 1450 ms) with that of the 2nd target (1200 ms). They pressed one key when they felt the 1st target was longer than the 2nd, and pressed another to indicate the reverse (those keys for the temporal judgment task were different from one used for the key-press actions). No time limitation was imposed.

In the interval condition, basic structures of a trial were same as the duration condition except that an amount of time (that should be compared in the temporal judgment task) was defined as an interval between two brief flashes. As shown in **Figure 1B**, one trial involved four brief flashes of a white disk. The duration of each flash was 17 ms (note that, because we used a CRT monitor, actual duration of the flash was about 2.5 ms in full width at half maximum, as measured by a photodetector and an oscilloscope). Subjects compared an interval (stimulus onset asynchrony or SOA) between the 1st and 2nd flashes (1st target) with that between the 3rd and 4th flashes (2nd target). The SOA in the 1st target ranged from 950 – 1450 ms while SOA in the 2nd target was fixed at 1200 ms. As the duration condition, an instruction screen of “Release and Repress” required subjects to perform the release and repress movements as quickly as possible in response to the 2nd flash (action trial). No release action was necessary in the no-action trial.

Both in the duration and interval conditions, a combination of two types of trials (action/no-action) with six durations (or SOAs) of the 1st target (950, 1050, 1150, 1250, 1350, and 1450 ms) produced 12 conditions. One experimental session contained 48 trials in which those 12 types of trials were randomly intermixed. Subjects performed six sessions, three for the duration and the other three for the interval conditions. An order of the two conditions was counterbalanced across subjects.

We instructed subjects to maintain the fixation throughout the trial. Changes in their eye positions were monitored and recorded at 250 Hz using the EyeLink CL system (SR Research) and the Eyelink Toolbox on Matlab (Cornelissen, Peters, & Palmer, 2002).

2.1.3. Data analyses

To investigate an effect of action preparation on time perception, we compared a subjective time for the 1st target between the action and no-action trials. Specifically, we measured the percentage of trials in which subjects indicated the 1st target as longer than the 2nd (%"1st-longer"). As shown in **Figure 2A and 2B**, the %"1st-longer" generally increased as a function of physical duration (or SOA) of the 1st target (950 – 1450 ms). We fitted this increase by a psychometric sigmoid function (Noguchi, Shimojo, Kakigi, & Hoshiyama, 2011; Suzuki, Wolfe, Horowitz, & Noguchi, 2013):

$$F(x) = min + (max - min)/[1 + e^{-a(x-b)}],$$

where x is the duration (or SOA) of the 1st target (in a unit of milliseconds), and a and b are free parameters estimated by the Nelder-Mead method. The *max* and *min* indicate the maximum and minimum %"1st-longer" over the six durations (or SOAs) of the 1st target (950 - 1450 ms). The effect of action preparation on subjective time was evaluated by comparing 50%-thresholds (**Fig. 2C**) of the psychometric curves between the action and no-action trials. If the action preparation induced a dilation of subjective time (Hagura et al., 2012), this would increase %"1st-longer" at all durations (or SOAs) of the 1st target, resulting in a leftward shift of the sigmoid function and a lower 50%-threshold.

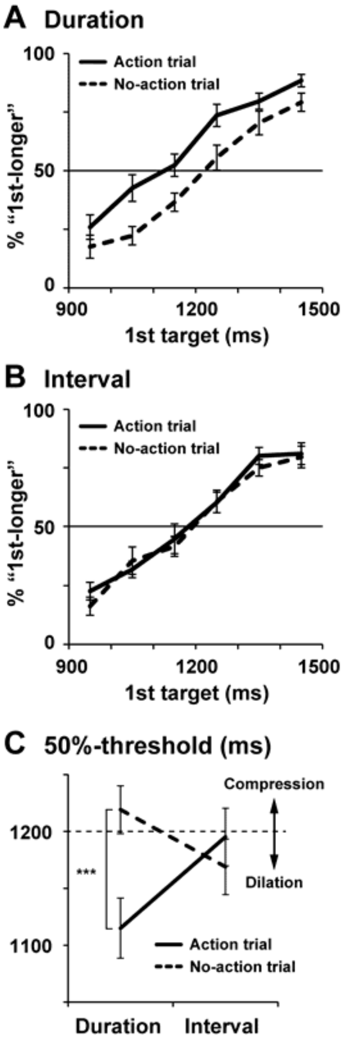

Figure 2. Results of Experiment 1. (**A**) Psychometric curves of the temporal judgment task in the duration condition. Percentages that subjects reported the 1st target as longer than the 2nd target (%"1st-longer") were plotted as a function of actual duration of the 1st target (950 – 1450 ms). Data in the action and no-action trials are shown in solid and dotted lines, respectively. (**B**) Psychometric curves in the interval condition. (**C**) The points of subjective equality (50%-thresholds) of the psychometric curves. Action preparation dilated subjective time for the 1st target in the duration condition but not in the interval condition. Error bars denote SEs across all subjects. ***$p < 0.001$.

2.2. Results and discussion

We first analyzed how quickly subjects performed the release and repress actions.

Means and SEs (across subjects) of reaction times (an interval from an end of 1st target to a completion of the release and repress movements) were 398.9 ± 12.1 ms in the duration and 385.4 ± 10.8 ms in the interval conditions. No significant difference was observed between the two conditions ($t(17) = 1.29$, $p = 0.22$, Cohen's $d = 0.28$).

Figure 2A and 2B shows psychometric curves for the temporal judgment task averaged across all subjects. Solid and dotted lines indicate changes of the %"1st-long" in the action and no-action trials, respectively. A three-way repeated-measured ANOVA of condition (duration/interval) × action (action/no-action) × length of the 1st target (950 – 1450 ms) indicated significant main effects of action ($F(1,17) = 21.63$, $p < 0.001$, $\eta^2 = 0.56$) and 1st-target length ($F(1.7,28.5) = 75.0$, $p < 0.001$, $\eta^2 = 0.82$) as well as a significant interaction of condition × action ($F(1,17) = 11.89$, $p = 0.003$, $\eta^2 = 0.41$). To explore the condition × action interaction, we performed two-way ANOVAs separately for the two conditions. In the duration condition (**Fig. 2A**), a two-way ANOVA of action (action/no-action) × durations of the 1st target (950 – 1450 ms) revealed a significant main effects of action ($F(1,17) = 32.59$, $p < 0.001$, $\eta^2 = 0.66$) and a main effect of durations ($F(2.4,41.3) = 54.56$, $p < 0.001$, $\eta^2 = 0.76$). No interaction between those two factors was observed ($F(5,85) = 1.44$, $p = 0.22$, $\eta^2 = 0.08$). The main effect of action indicated that a dilation of subjective time during action preparation (Hagura et al., 2012) was successfully replicated in the present study. On the other hand, the same 2 × 6 ANOVA in the interval condition (**Fig. 2B**) yielded a significant main effect of six SOAs ($F(2.0,34.5) = 52.34$, $p < 0.001$, $\eta^2 = 0.76$), although no effect of action ($F(1,17) = 0.73$, $p = 0.41$, $\eta^2 = 0.04$) or an interaction ($F(5,85) = 1.03$, $p = 0.41$, $\eta^2 = 0.06$) was obtained.

Figure 2C shows 50%-thresholds of four psychometric curves in **Figure 2A** and **2B**. A two-way ANOVA of condition (duration/interval) and action (action/no-action) revealed a significant main effect of action ($F(1,17) = 8.62$, $p = 0.009$, $\eta^2 = 0.34$) and a significant interaction of two factors ($F(1,17) = 17.20$, $p = 0.001$, $\eta^2 = 0.50$). No main effect of condition was observed ($F(1,17) = 0.65$, $p = 0.43$, $\eta^2 = 0.04$). A post-hoc comparison with a correction of multiple comparisons (Bonferroni method) showed a significant difference between the action and no-action trials in the duration condition ($p = 0.0003$), but not in the interval condition ($p = 0.41$). Those results of %“1st-long” and 50%-thresholds indicated that a dilation of time was selectively induced in the duration condition.

We also analyzed precisions of task performances using the data of slopes of fitted sigmoid functions (parameter a in the equation above). A steeper slope of the psychometric function indicates higher accuracy of the temporal judgment task. Those values averaged across all subjects (± SE) were 0.057 ± 0.028 (duration, action), 0.072 ± 0.034 (duration, no-action), 0.116 ± 0.057 (interval, action), and 0.092 ± 0.055 (interval, no-action). A two-way ANOVA indicated no main effect or interaction (main effect of condition: $F(1,17) = 0.63$, $p = 0.44$, $\eta^2 = 0.035$, main effect of action: $F(1,17) = 0.01$, $p = 0.91$, $\eta^2 = 0.001$, interaction of condition and action: : $F(1,17) = 1.78$, $p = 0.20$, $\eta^2 = 0.095$).

Several previous studies have suggested that predictability of action outcomes played a key role in sensory-motor interactions (Gutteling et al., 2015) and action-related time distortion (Press et al., 2014). In case of the present study, subjects were unable to predict action timings (duration or SOA of the 1st target) in the first several trials of each condition, because a length of the 1st target was randomly varied from 950 to 1450 ms (low predictability). This range of variation (950 - 1450 ms), however, was fixed throughout all sessions of each condition, which enabled subjects to predict an approximate length of the 1st target in trials of the last session (high predictability). We thus investigated how predictability of visual events affected time sensations by comparing data (%“1st-long”) between the first and third (last) sessions of each condition (**Fig. 3**). A four-way ANOVA of session (first/last) × condition (duration/interval) × action (action/no-action) × length of the 1st target (950 – 1450 ms) indicated a significant main effect of session (first < third, $F(1,17) = 13.16$, $p = 0.002$, η^2

= 0.44), as well as a main effect of action ($F(1,17) = 16.12$, $p = 0.001$, $\eta^2 = 0.49$), a main effect of the 1st-target length ($F(2.1,36.3) = 66.29$, $p < 0.001$, $\eta^2 = 0.80$), and an action × condition interaction ($F(1,17) = 11.46$, $p = 0.004$, $\eta^2 = 0.40$). An increased %"1st-long" from first (49.9 %) to third (54.1 %) sessions suggests that higher predictability of visual events (in the last session) dilated a perceived length of the 1st target, indicating an involvement of predictability in the present study. Our data in the first session, however, also suggest that time dilation in the present study can be induced even under low predictability of action timings.

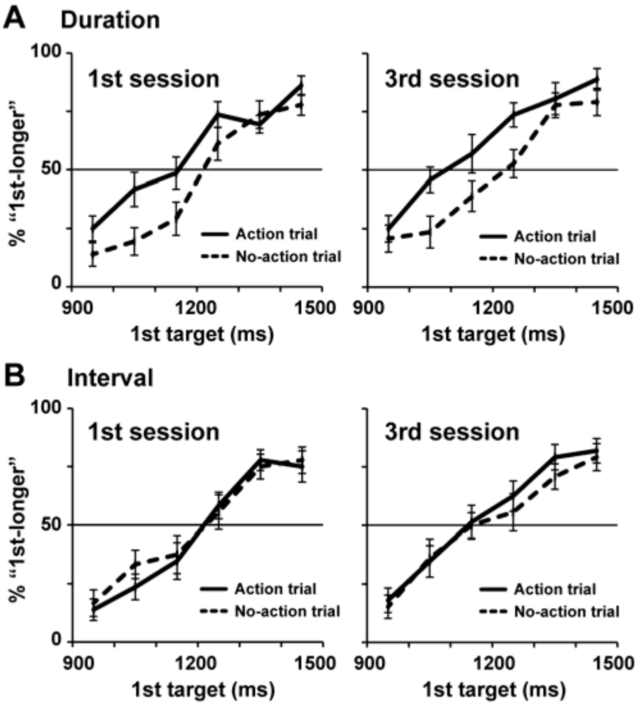

Figure 3. Results of Experiment 1. Changes in %"1st-longer" in the first and last (third) sessions are separately shown.

3. Experiment 2

Experiment 1 showed that subjective time of a continuous stimulus (stimulus period) was dilated by action preparation (**Fig. 2A**) while that of an inter-stimulus interval (no-stimulus period) was not (**Fig. 2B**). Those results were consistent with our hypothesis in **Introduction** that an action-related distortion of time greatly depends on the presence/absence of continuous inputs during a period to be estimated. Some previous studies, however, indicated separate neural systems of time processing between sub-second and supra-second scales (Lewis & Miall, 2003; Mauk & Buonomano, 2004). For example, Lewis and Miall (2003) proposed a distinction between the 'automatic' timing system involved in the measurement of sub-second (< 1 sec) intervals and the 'cognitively controlled' timing system for estimating supra-second (> 1 sec) intervals. The former mainly draws on neural processing in motor-related regions in the brain while the latter depends on brain areas associated with attention and working memory (e.g. prefrontal and parietal regions). Because lengths of target stimuli in Experiment 1 were 950 – 1450 ms (supra-second range), it might be necessary to investigate whether our results in Experiment 1 hold true for durations and intervals of a sub-second range. We therefore conducted Experiment 2 in which subjects estimated and compared lengths of target stimuli of around 300 ms.

3.1. Methods

Sixteen subjects participated in Experiment 2. Basic procedures were identical to Experiment 1 except for the following three points. First, we used target stimuli of a sub-second range. The duration (or interval) of 1st target was set at 183, 233, 283, 317, 367, or 417 ms, while that of 2nd target was fixed at 300 ms (unknown to subjects). Second, although subjects in Experiment 1 had to complete release and repress movements within 500 ms in action trials, the limit was extended into 600 ms in Experiment 2. This was based on our preliminary experiment that a use of shorter (sub-second) target stimuli produced longer reaction times compared to Experiment 1 (see below). Third, each experimental session in Experiment 2 contained 60 trials in which 12 types of trials (action/no-action × six durations or SOAs of the 1st target) were randomly intermixed. Subjects performed four sessions, two for the duration and the other two for the interval conditions.

3.2. Results and discussion

Means and SEs of reaction times were 437.3 ± 14.5 ms in the duration and 451.2 ± 13.1 ms in the interval conditions. No significant difference was observed between the two conditions ($t(15) = 1.22$, $p = 0.24$, $d = 0.25$). **Figure 4A and 4B** shows psychometric curves for a temporal judgment task. A three-way ANOVA of condition (duration/interval) × action (action/no-action) × length of the 1st target (183 – 417 ms) indicated significant main effects of action ($F(1,15) = 11.67$, $p = 0.004$, $\eta^2 = 0.44$) and 1st-target length ($F(2.5,38.2) = 285.1$, $p < 0.001$, $\eta^2 = 0.95$) as well as significant interactions of condition × 1st-target length ($F(5,75) = 4.32$, $p = 0.002$, $\eta^2 = 0.22$) and condition × action × 1st-target length ($F(5,75) = 2.56$, $p = 0.034$, $\eta^2 = 0.15$). To explore the 3-way interaction (condition × action × 1st-target length), we performed two-way ANOVAs separately for the two conditions. In the duration condition, the ANOVA indicated significant main effects of action ($F(1,15) = 12.84$, $p = 0.003$, $\eta^2 = 0.46$) and 1st-target length ($F(3.0,44.9) = 219.0$, $p < 0.001$, $\eta^2 = 0.94$) as well as a significant interaction of the two factors ($F(3.1,46.5) = 3.28$, $p = 0.028$, $\eta^2 = 0.18$). In the interval condition, only a significant main effect of the 1st-target length ($F(2.8,42.4) = 190.0$, $p < 0.001$, $\eta^2 = 0.93$) was observed.

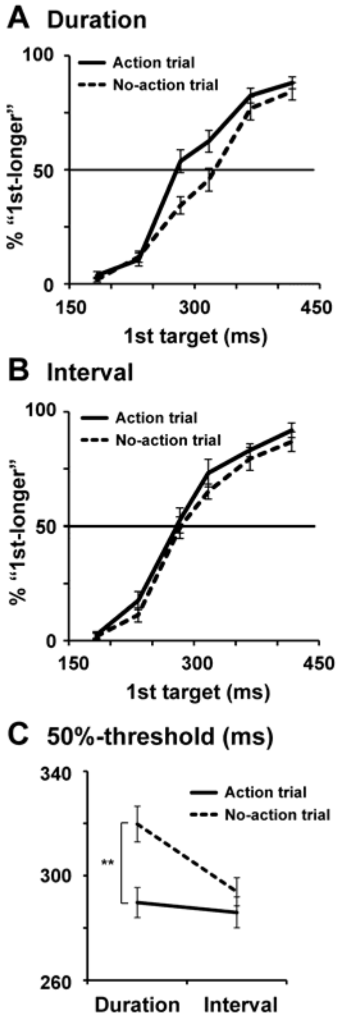

Figure 4. Results of Experiment 2 using target stimuli in a sub-second scale (183 - 417 m). (**A**) Psychometric curves of the temporal judgment task in the duration condition. (**B**) Psychometric curves in the interval condition. (**C**) The points of subjective equality (50%-thresholds). As Experiment 1, action preparation dilated subjective time for the 1st target only in the duration condition. Error bars denote SEs. $^{**}p < 0.01$.

A two-way ANOVA on 50%-thresholds (**Fig. 4C**) revealed a significant main effect of condition (duration/interval, $F(1,15) = 6.21$, $p = 0.025$, $\eta^2 = 0.29$) and action (action/no-action, $F(1,15) = 11.53$, $p = 0.004$, $\eta^2 = 0.43$). Importantly, a significant interaction of the two factors was also observed ($F(1,15) = 7.51$, $p = 0.015$, $\eta^2 = 0.33$). A post-hoc comparison with a correction of multiple comparisons showed a significant difference between the action and no-action trials in the duration condition (p = 0.0016), but not in the interval condition (p = 0.50). These results resemble those in Experiment 1, showing that an action-related dilation was induced in the duration condition but not the interval condition.

We also analyzed precisions of task performances. The slope of fitted psychometric function (an index for task accuracy) was 0.040 ± 0.003 (duration, action), 0.034 ± 0.003 (duration, no-action), 0.073 ± 0.020 (interval, action), and 0.052 ± 0.015 (interval, no-action). The two-way ANOVA indicated no main effect or interaction (main effect of condition: $F(1,15) = 3.92$, $p = 0.066$, $\eta^2 = 0.207$, main effect of action: $F(1,15) = 1.09$, $p = 0.31$, $\eta^2 = 0.068$, interaction of condition and action: $F(1,15) = 0.33$, $p = 0.57$, $\eta^2 = 0.022$).

4. Experiment 3

In Experiments 1 and 2, we compared the duration and interval conditions that shared basic structures. The two conditions involved the same set of stimuli (white disk at the fovea), actions (release and repress movements), and lengths of time to be estimated (950 – 1450 ms in Exp. 1 and 183 – 417 ms in Exp. 2). One might argue, however, that there were still some differences between the two conditions. For example, subjects released a key in response to an offset of a white disk (an onset of a fixation-only screen) in the duration condition. In other words, an action-triggering event in the duration condition was an onset of the fixation-only screen, which was continuously presented for a long time (1500 ms) while actions were executed. In contrast, an action-triggering event in the interval condition was an onset of the 2nd flash. The duration of the 2nd flash was 17 ms, rapidly disappearing from the screen before actions were completed. The duration and interval conditions were thus *not* balanced in terms of continuity (temporal constancy) of action triggering events, which might produce the dilation effect selectively observed in the duration condition (**Fig. 2** and **Fig. 4**).

To eliminate this possibility, we tested in Experiment 3 a new type of interval condition where the length of the 2nd and 4th flashes was extended from 17 ms to 700 ms (**Fig. 5A**). Subjects released a key in response to an onset of the 2nd flash, completing all actions (release and repress) while the 2nd flash remained on the screen. If continuity of an action-triggering event is critical, an action-related dilation would be observed in this new type of interval condition, as the duration condition in Experiments 1 and 2.

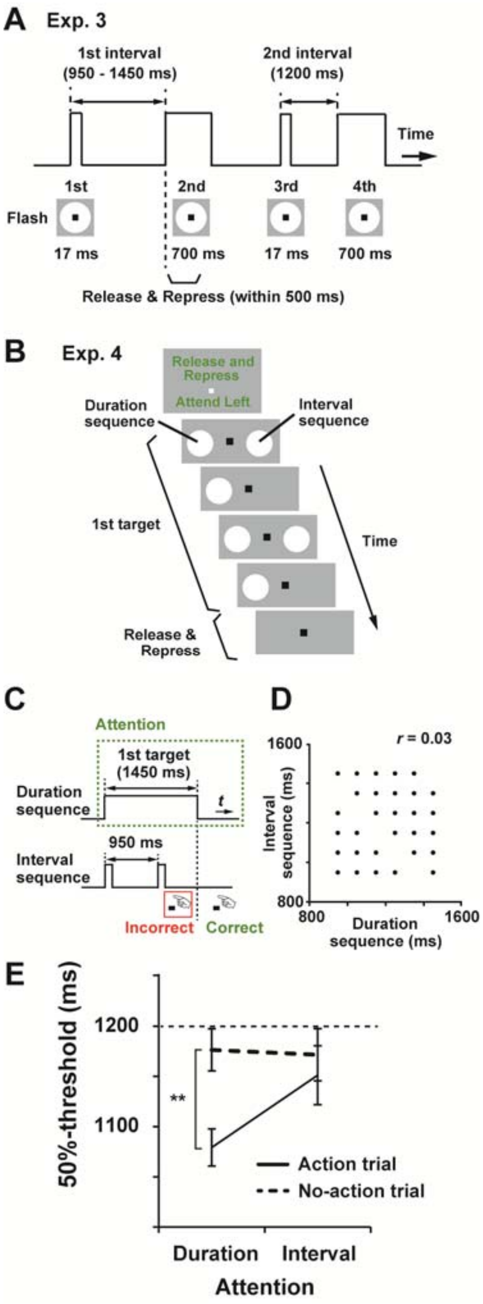

Figure 5. Experiments 3 and 4. (**A**) Structures of one trial in Experiment 3. Lengths of the

2nd and 4th flashes in the interval condition were set at 700 ms so that subjects completed the release and repress movements while the 2nd flash remained on the screen. (**B** and **C**) Structures of 1st-target period in Experiment 4. Stimulus sequences in the duration and interval conditions were simultaneously shown to the left and right of a fixation point. Subjects attended to the duration sequence in one experimental session but attended to the interval sequence in another session. Since lengths of the two sequences were different in most trials (e.g. 1450 ms in the duration sequence but 950 ms the interval sequence, as shown in panel **C**), subjects had to perform release and repress movements in an appropriate time window, attending to the sequence indicated by an instruction. (**D**) A within-trial correlation of 1st-taget lengths between the duration and interval sequences in one experimental session (60 trials). (**E**) Results of Experiment 4. Action preparation reduced the 50%-thresholds of %“1st-longer”only when subjects attended to the duration sequence. Error bars denote SEs. $^{**}p < 0.01$.

4.1. Methods

Thirteen subjects participated in Experiment 3. All procedures were identical to the interval condition of Experiment 1 except that the duration of the 2nd and 4th flash was extended to 700 ms. In action trials, subjects were asked to complete release and repress movements within 500 ms after an onset of the 2nd flash. Each experimental session comprised 60 trials in which 12 types of trials (action/no-action × six SOAs of the 1st target) were randomly intermixed. Subjects performed two sessions.

4.2. Results and discussion

Means and SEs of reaction times were 347.6 ± 5.0 ms (release time: 249.1 ± 2.8 ms, repress time: 98.6 ± 4.4 ms). The 50%-thresholds of %”1st-longer” were 1159.7 ± 32.8 ms in action and 1215.1 ± 25.8 ms in no-action trials. No significant difference was observed between the two types of trials ($t(12) = 1.67$, $p = 0.12$, $d = 0.52$). These results indicated that continuity of an action-triggering event was *not* critical for the dilation effect in the duration condition of Experiments 1 and 2.

5. Experiment 4

Although results in Experiment 3 eliminated the possibility that time dilation in the duration condition was caused by a continuous presentation of an action-triggering event, one might still argue that structures of trials in the duration condition were different from those in the interval condition. Specifically, trials in the duration condition involved two long flashes, while those in the interval condition involved four brief flashes. Those differences in visual inputs might produce an action-related dilation selectively observed in the duration condition.

To address this issue, we conducted Experiment 4 in which visual inputs between the duration and interval conditions were completely matched. As shown in **Figure 5B and 5C**, the screen in Experiment 4 contained two sequences of stimuli (one for the duration task and another for the interval task) simultaneously presented around the fixation point. Subjects attended to the sequence for the duration task in one experimental session but attended to the sequence for the interval task in another session. These procedures enabled a perfect control of visual inputs in which only attention of subjects was switched across the two conditions.

5.1. Methods

Fourteen subjects participated in Experiment 4. In a half of the subjects, a stimulus sequence for the duration task (duration sequence) was presented at a location to the left of a fixation point (eccentricity: 3.135 deg), while that for the interval task (interval sequence) was presented to the right. Locations for the two sequences were reversed in the other half of the subjects. Structures of each sequence were identical to those in Experiment 1; the duration/interval of the 1st target randomly varied from 950 to 1450 ms (**Fig. 5C**) while that of the 2nd target was fixed at 1200 ms. At the beginning of each session, we instructed subjects to which sequence they should attend (left or right). This information about the to-be-attended sequence was also indicated by an instruction screen at the beginning of every trial (**Fig. 5B**). Subjects performed the duration task when their attention was directed to the duration sequence and performed the interval task when directed to the interval sequence. Since lengths of the two sequences in the 1st-target period were different in most trials (**Fig. 5D**), subjects had to perform release and repress movements in an appropriate time window, attending to the sequence indicated by the instruction (**Fig. 5C**). If they erroneously performed the interval task when they should attend to the duration sequence, for example, this would produce a large amount of error trials due to release and repress movements in a wrong time window. Subjects performed four sessions (two for the duration task and two for the interval task) of 60 trials, with an order of the duration and interval sessions counterbalanced across subjects. Other details were identical to Experiment 1.

5.2. Results and discussion

Means and SEs of reaction times were 391.7 ± 6.0 ms (release time: 284.9 ± 5.5 ms, repress time: 106.8 ± 3.8 ms) for the duration (attending-to-the-duration-sequence) condition and 375.1 ± 11.3 ms (release time: 271.6 ± 10.0 ms, repress time: 103.5 ± 3.8 ms) for the interval condition. No significant difference between the duration and interval conditions was observed for release time ($t(13) = 1.23$, $p = 0.24$, $d = 0.44$), repress time ($t(13) = 1.83$, $p = 0.09$, $d = 0.23$), or total reaction time ($t(13) = 1.49$, $p = 0.16$, $d = 0.49$). The 50%-thresholds of %"1st-longer" were shown in **Figure 5E**. Action preparation significantly reduced the threshold in the duration condition ($t(13) = 4.13$, corrected $p = 0.002$, $d = 1.32$), while no difference in thresholds was observed in the interval condition ($t(13) = 0.71$, uncorrected $p = 0.49$, $d = 0.20$).

6. Experiment 5

Experiments 1-4 showed that action preparation dilated a subjective length of a continuous stimulus (stimulus period) but not for an inter-stimulus interval (no-stimulus period). In a final experiment, we used a light-emitting diode (LED, **Fig. 6A**) and tested how action preparation affected subjective time of a no-stimulus period when it was simultaneously given (mixed) with stimulus periods. One of such situations is illustrated in **Figure 6B** where the continuous lighting of an LED transiently goes off. In this case, a brief disappearance (gap, no-stimulus period) is preceded and followed by stimulus periods (pre-gap and post-gap periods) that would be dilated by action preparation. How the brain feels time for a no-stimulus period when it is mixed into a sequence of stimulus periods? One possibility is that action preparation dilates a whole sequence of events, causing an overestimation of both stimulus (pre-gap and post-gap) and no-stimulus (gap) periods (left panel of **Fig. 6C**). This might be consistent with previous views assuming a uniform change of subjective time (uniform dilation or uniform compression) by actions. In contrast, our results in Experiments 1-4 showed a distinction between stimulus and no-stimulus periods. This distinction suggests another possibility that action preparation does *not* change subjective time of a gap even though it dilates the pre-gap and post-gap periods (right panel of **Fig. 6C**). Such results would show a new type of time distortion in which action changes perceived time in a non-uniform manner, depending on continuity of sensory inputs.

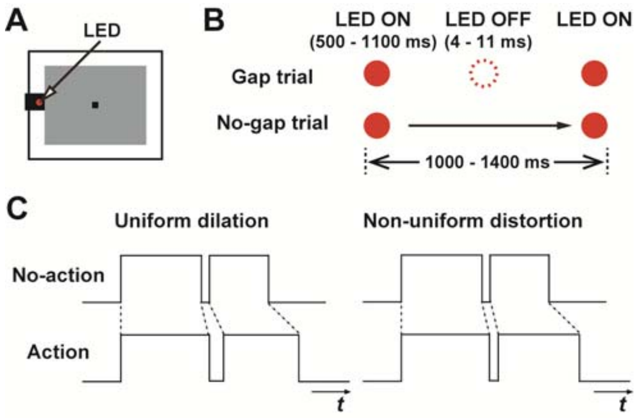

Figure 6. Experiment 5. (**A**) Experimental settings. A laser-emitting diode (LED) was placed in a peripheral visual field of subjects (on the left or right edge of the CRT monitor, eccentricity: 16 deg). (**B**) Gap detection task. Subject reported whether continuous lighting of the LED (1000 – 1400 ms) had a transient disappearance (gap, 4 - 11 ms) or not. (**C**) Possible results. If the action-related dilation (shown by Exp. 1 and 2) works in a uniform manner (left panel), this would extend the duration of both stimulus and no-stimulus periods, producing an improved performance of the gap detection task in the action than no-action conditions. In contrast, if motor commands selectively dilate a stimulus period, a subjective length of a gap would be unaffected by action preparation (non-uniform distortion of time). Performances of the gap detection task in the action trials would be thus comparable to those in the no-action trials.

6.1. Methods

Nineteen subjects participated in Experiments 5. To measure a subjective length of a no-stimulus period embedded in a stimulus period, we used the gap-detection task (Kanai, Sheth, & Shimojo, 2007; Treutwein & Rentschler, 1992). Each trial in this task involved a long-lasting stimulus, continuous lighting of an LED attached on the left (N = 9) or right (N = 10) edge of a CRT monitor (eccentricity: 16 deg, **Fig. 6A**). In a half of trials, the LED went off briefly (gap) at a random time from a lighting onset (gap trials). A length of the gap was 4, 6, 8, or 11 ms. Pre-gap and post-gap periods ranged from 500 – 1100 ms and 289 – 496 ms, respectively. Those gap trials were intermixed with another type of trials in which an LED was continuously lit for 1000-1400 ms (no-gap trials). Subjects discriminated the gap from the no-gap trials while they prepared for the release and repress actions. If action preparation induces a uniform dilation of subjective time (**Fig. 6C**, left), this would dilate a gap as well as pre-gap and post-gap periods, resulting in an improved performance of the gap-detection task (e.g. increase in a detection rate of the gap). In contrast, if action preparation changes time perception in a non-uniform manner (**Fig. 6C**, right), no dilation would be induced in a no-stimulus period. Performances of the gap detection task in the action trials would be thus comparable to those in the no-action trials.

Figure 7 illustrates three conditions in Experiment 5. In the action condition (**Fig. 7A**), a trial started with an instruction of “Release and Repress”. Pressing a key eliminated the message and changed a fixation color from white to black (fixation screen, 500 ms). Subjects then observed lighting of an LED (in their peripheral visual field) to discriminate the gap from the no-gap trials with their hand pressing the key. When the LED completely went off, a green disk (2.2 deg in diameter) appeared on the CRT at an adjacent position to the LED (eccentricity: 14.1 deg), which prompted subjects to perform release and repress movements. When both actions were successfully done within 500 ms, a task screen asked whether they had found a gap of the LED. Subjects pressed one key when they had perceived a gap and pressed another when not (no time limitation was imposed). In the second (no-action) condition (**Fig. 7B**), basic structures of a trial were the same as the action condition, except that a message for an instruction was “Keep Pressing” and that subjects kept pressing a key until the task screen (“Gap or No-Gap? ”) was presented.

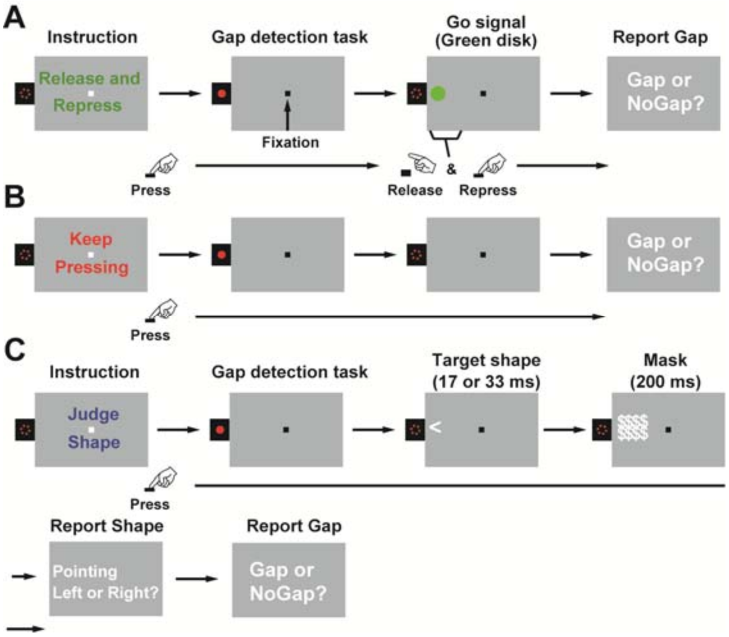

Figure 7. Three types of trials in Experiment 5. (**A**) Action trial. Subjects viewed lighting of an LED while preparing for release and repress movements in response to a green disk (that was presented on a CRT monitor when the LED completely went off). They answered whether the LED had involved a gap or not at the end of each trial. (**B**) No-action trials. No release or repress movement was necessary and subjects simply performed the gap-detection task. (**C**) Judge shape (JS) trials. In addition to the gap-detection task, subjects discriminated a pointing direction (left or right) of a target stimulus ("<" or ">", shape task) followed by a mask (an array of "$"). These JS trials resembled a dual-task design in the action trials (panel **A**) but required no key actions. An order of two tasks (the gap-detection and shape tasks) was counterbalanced across subjects. Performances of the gap detection task in the action trials were compared with those in the no-action and JS trials, to investigate how action preparation affected a subjective length of a gap (no-stimulus period).

Although our main purpose in Experiment 5 was to compare performances of the gap-detection task between the action and no-action trials, one might argue that those two types of trials were not balanced in terms of task loads and attention; subjects had to detect a gap of the LED while preparing release and repress movements in the action condition (dual-task design), whereas they can fully focus on the gap-detection task in the no-action condition (single-task design). We therefore set a third type of trials (judge shape or JS condition, **Fig. 7C**) where subjects performed two tasks in every trial. In this condition, two visual stimuli were sequentially presented on the CRT monitor just after an offset of the LED. The first stimulus (shape) was either "<" or ">", presented for 17 or 33 ms (variable across trials). The second stimulus (mask) consisted of six "$"s arranged in a two-by-three array (200 ms). The shape and mask were displayed at a peripheral position adjacent to the LED (eccentricity: 14.1 deg), and there was no inter-stimulus interval from an offset of the shape to an onset of the mask. Subjects judged a pointing direction of the shape (left or right, shape task) in addition to detecting a gap of the LED (dual-task design).

One experimental session comprised 96 trials, 32 trials for each of the three (action, no-action, and JS) conditions. The 32 trials consisted of 16 gap trials (four trials for each of four gap lengths, 4, 6, 8, and 11 ms) and 16 no-gap trials. Subjects conducted four experimental sessions where all types of trials were randomly intermixed. We monitored eye positions of subjects throughout the trials at 250 Hz. An error message was presented when subjects averted their eyes from the fixation point or when they performed key-pressing actions incorrectly. Those error trials were repeated later in the same experimental session.

For data analyses, we computed hit and false-alarm rates in the gap-detection task. Those rates were then converted into a sensitivity measure (d') in the signal detection theory and compared among the three (action, no-action, and JS) conditions.

6.2. Results

Figure 8A shows the d' in the gap-detection task (see **Fig. 8B** for scatter plots). A one-way ANOVA yielded a significant main effect across the three conditions ($F(2,36) = 7.27$,

$p = 0.002$, $\eta^2 = 0.29$), and post-hoc comparisons (corrected for multiple comparisons with the Bonferroni method) indicated significant differences in action vs. no-action (corrected $p = 0.006$) and action vs. JS ($p = 0.04$), but not in no-action vs. JS ($p = 0.66$). Those results showed smaller *d'* in action compared to the other two conditions. **Figure 8C** shows changes of the *d*' across the four lengths of gap (4 -11 ms). Thresholds of the gap length (ms) at $d' = 2$ are displayed in **Figure 8D.** Consistent with **Figure 8A**, we found a larger threshold in action condition compared to those in no-action ($t(18) = 2.30$, $p = 0.034$, $d = 0.25$) and JS ($t(18) = 2.48$, $p = 0.023$, $d = 0.21$) conditions.

Finally, we showed results of the shape task in the JS condition (**Fig. 8E**). Accuracy (mean ± SE across subject) was 58.99 ± 2.13 % for a target shape of 17 ms and 73.79 ± 4.05 % for a target shape of 33 ms, suggesting that the shape task was highly demanding to subjects. The accuracy for the 33-ms target, however, was significantly higher than that for the 17-ms target ($t(18) = 3.89$, $p = 0.001$, $d = 1.05$), which indicates that subjects were seriously engaged in the demanding task.

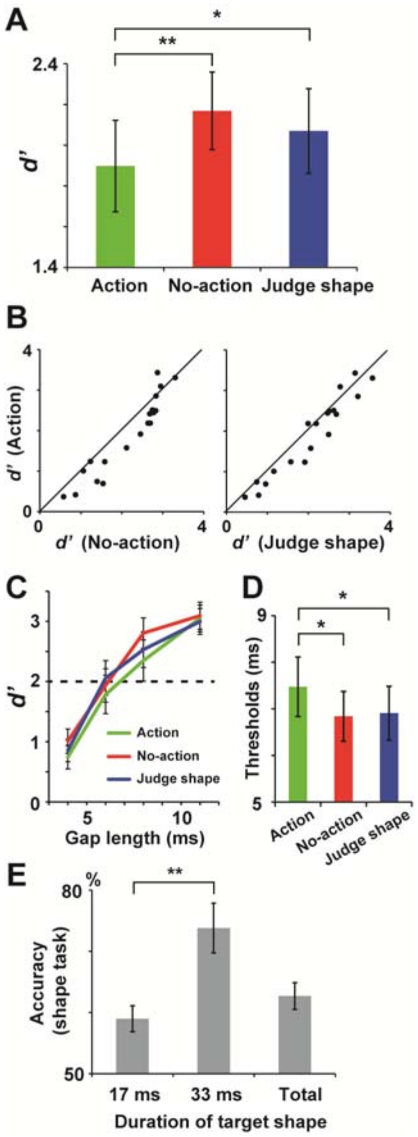

Figure 8. Results of Experiment 5. (**A**) A sensitivity measure (*d'*) to a gap (obtained from hit and false-alarm rates in a gap-detection task, see texts for details). The reduced *d'*s in the action trials compared to the no-action and JS trials indicate that subjective time for a gap was compressed by action preparation. (**B**) Paired comparisons of *d'*s. Each point shows a data of one subject. Both in the action vs. no-action trials (left panel) and the action vs. JS trials (right panel), most points are located below a 45-degree line, indicating that *d'*s in the action trials were smaller than those in the no-action and JS trials. (**C**) Changes in *d*' as a function of four gap lengths (4, 6, 8, and 11 ms). (**D**) Thresholds of the gap length (ms) at *d*' = 2. (**E**) Accuracy of the shape task in the JS trials (chance level: 50 %). Increasing the duration of a target shape

(“<” or “>”) from 17 to 33 ms improved task accuracy. Error bars denote SEs across all subjects. $*p < 0.05$, $*p < 0.01$.

6.3. Discussion

Our data in Experiment 5 showed a decreased sensitivity to a gap in the action than no-action conditions. Although these results suggest a compression of a no-stimulus period by action preparation, there are some points that should be noted. First, the *d’* was an index for sensitivity to the gap, not a direct measure for a subjective length of time. The decreased *d’* thus does not necessarily indicate a compression of a gap period. Second, it was unclear whether attention to tasks was perfectly controlled among the three conditions. A smaller *d’* in the JS than the no-action condition (**Fig. 8A**) suggested that the *d’* can be modulated by an amount of attention assigned to the gap-detection task. If the action task drew more attention away from the gap task than the shape task did, the decreased *d’* in action condition might be explained by reduced attention to the gap task in that condition. Therefore, our present data were not sufficient to demonstrate an action-related compression of a no-stimulus period. An implication of Experiment 5, however, was that a subjective length of a no-stimulus period was *not* dilated by action preparation even when it was mixed into a sequence of stimulus periods. This supported a possibility of the non-uniform transformation of time by action preparation (right panel of **Fig. 6C)**.

7. General discussion

In the present study, we investigated an action-related distortion of time by focusing on the presence of continuous inputs during an estimation period. Results of five experiments showed that action preparation extended the duration of a single long-lasting stimulus (stimulus period) but did not affect a time sensation for an inter-flash interval (no-stimulus period). Those results suggested a new possibility that action preparation distorts subjective time in a non-uniform manner.

What neural mechanisms underlie this non-uniform transformation of time? Although it remains unclear how sensations (representations) of time are created in the brain (Gibbon, Malapani, Dale, & Gallistel, 1997; Harrington, Haaland, & Knight, 1998; Ivry & Spencer, 2004; Mauk & Buonomano, 2004), it is highly possible that a time representation for a sensory event is built on neural responses in the sensory areas induced by that event (Indeed, some researchers assume modality-specific neural mechanisms for time perception (Johnston, Arnold, & Nishida, 2006; Penney, Gibbon, & Meck, 2000; Wearden, Edwards, Fakhri, & Percival, 1998; Yuasa & Yotsumoto, 2015)). One explanation for the present results is that action preparation induced a dilation of time by interacting with those neural responses in the sensory areas. For example, action preparation is known to modulate neural activity in the visual cortex (Gutteling et al., 2015), suggesting that motor commands amplify neural responses to a visual stimulus presented in a pre-action period. Since a visual stimulus inducing stronger neural responses is perceived longer (Noguchi & Kakigi, 2006), this amplification of neural responses by motor commands would cause overestimation of time (action-related dilation). In contrast, the interaction between motor commands and visual responses is not applicable to no-stimulus period, because a lack of a stimulus in this period induces little or no visual responses in the brain. No dilation of time is therefore induced for no-stimulus periods, as was observed in the interval condition.

Many studies have indicated that the “action-relevance” of sensory inputs plays a key role in inducing sensory-motor interactions. In studies by Gutteling et al. (Gutteling, Kenemans, & Neggers, 2011; Gutteling, Park, Kenemans, & Neggers, 2013), for example, subjects were asked to grasp or point to a bar stimulus while performing an orientation discrimination task. Perceptual sensitivity to orientation changes was more enhanced by preparation of a grasping action (for which orientation information was important), compared to that of a pointing action (for which orientation information was not important). In other words, action preparation mainly facilitated the processing of visual features relevant to that action. In this sense, an action-related dilation of time in the present study might be somewhat surprising, because visual features of our target stimulus (white disk) was not directly associated with actions (release and repress movements of a key). Recent studies, however, indicated that action can affect perception of a stimulus even when that stimulus was irrelevant to a motor task (Jia, Shi, Zang, & Muller, 2015; Tomassini, Spinelli, Jacono, Sandini, & Morrone, 2015). For example, preparation of reaching movements to a bar modulated a contrast sensitivity to a visual stimulus (Gabor patch) totally unrelated to the movements (Tomassini et al., 2015). Those recent results suggest a possibility that motor commands can influence the neural processing in the visual cortex even though the processed features were not directly associated with actions, although such sensory-motor interactions would be maximized by a high relevance to actions.

One limitation of the present study was that all experiments were conducted in a pre-action design in which target stimuli for time estimation were presented before actions. As described in **Introduction**, action is a complex process consisting of multiple stages (preparation, execution, and termination, etc.), each of which would involve different patterns of neural activity. Although we presently showed a time dilation selectively induced in a stimulus period, it should be elucidated in future studies whether this distinction between stimulus and no-stimulus periods holds true for other (during- and post-action) stages. Such studies would be of great help in resolving a controversy (dilation vs. compression) on how action changes a perception of time.

Finally, we will consider adaptive functions of a non-uniform transformation of time by action preparation. A previous study proposed that time dilation in a pre-action period reflects the brain function to increase temporal resolution of the sensory processing (Hagura et al., 2012). In planning of quick and ballistic movements, it is important for the brain to maximize opportunities to stop or change the planned movement before actual execution. Boosting a speed of visual processing clearly enhances an ability to adjust actions in accordance with changing environments. This mechanism of time dilation, however, also has a disadvantage, because it causes inaccurate perception of time by enlarging a difference between physical and subjective times. To achieve accurate time perception, it would be better for the brain not to dilate a period where no stimulus is presented. The dilation of time selectively induced in a stimulus period therefore might reflect a strategy by the brain to maximize the processing of the sensory information while minimizing erroneous perception of time.

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