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**PHYSICAL DELAY BUT NOT SUBJECTIVE DELAY DETERMINES LEARNING RATE
IN PRISM ADAPTATION**

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ABSTRACT

Timing is critical in determining the causal relationship between two events. Motor adaptation relies on the timing of actions and their results for determining which preceding control signals were responsible for subsequent error in the resulting movements. An artificially induced temporal delay in error feedback as short as 50 ms has been found to slow the learning rate of prism adaptation. Recent studies have demonstrated that our sense of simultaneity is flexibly adaptive when a persistent delay is inserted into visual feedback timing of one's own action. Therefore, judgments of "subjective simultaneity" (i.e. whether two events are simultaneous on a subjective basis) do not necessarily correspond to the actual simultaneity of physical events. We evaluated the effects of adaptation to a temporal shift of subjective simultaneity on prism adaptation by examining whether prism adaptation depends on physical timing or subjective timing. We found that after persistently experiencing an additional 100 ms delay in a pointing experiment, psychometric curves of the timing of judgments about the temporal order of touching and visual feedback were shifted by 40 ms, indicating that subjective simultaneity adapted. Next, while maintaining temporal adaptation, participants adapted to spatial displacement caused by a prism with and without an additional temporal delay in feedback. Learning speed was reliably predicted by physical timing but not by subjective timing. These results indicate that prism adaptation occurs independently of awareness of subjective timing, and may be processed in primary motor areas that are thought to have fidelity with temporal relations.

INTRODUCTION

Time differs from the three spatial dimensions in the sense that it flows only in one direction. It is unsurprising that the human perceptual and motor systems exploit this temporal unidirectionality. Inter-stimulus temporal order provides a crucial cue to the visual system in estimating a given motion stimulus (McKee, 1981; Ramachandran and Anstis, 1986), and to the auditory system in localizing a sound-source position (Knudsen and Konishi, 1978; Takahashi and Konishi, 1986). Time is most important in the motor control system, where appropriate movements require precisely coordinated timing of muscle activation (Miall et al., 1993; Rao et al., 1997; Ivry et al., 2002). It is also known that delayed visual feedback as short as a fraction of a second has deleterious effects on writing and drawing (Smith et al., 1960; Miall et al., 1985). Further, delayed auditory feedback of self-generated voice has been found to impair speech (Lee, 1950). Therefore, timely control of the musculoskeletal system and sensory feedback from periphery receptors are of vital importance both in perceiving the external environment and in coordinating body movements.

Temporal relationships play a crucial role not only in movement execution but also in movement adaptation, which involves learning the causal association between motor commands and subsequent errors. Among various cues for identifying causal relationships, sensory feedback is important for determining the temporal order and proximity among recent events. As such, an artificially induced delay in sensory feedback would be expected to affect how motor adaptation proceeds. An induced delay of visual feedback during prism adaptation, for example, has been found to decrease learning speed even with delays as short as 50 ms both in humans (Kitazawa et al., 1995) and monkeys (Kitazawa and Yin, 2002). Further, physiological experiments have

revealed that a precise spike timing between pre- and post-synaptic neurons determines how the synaptic strength between these neurons will be modified (i.e., potentiated or depressed) in the cortex (Markram et al., 1997; Yao and Dan, 2001; Froemke and Dan, 2002; Celikel et al., 2004), the hippocampus (Debanne et al., 1998; Watanabe et al., 2002; Wang et al., 2005) and basal ganglia (Fino et al., 2005; Pawlak and Kerr, 2008) of the mammalian brain, and also in fish (Bell et al., 1997). In the cerebellum, thought to function as a neural site for movement coordination and learning (Marr, 1969; Houk et al., 1996; Imamizu et al., 2000), synaptic strength between the parallel fibers and the Purkinje cells is maximally depressed when parallel-fiber activity is followed by climbing fiber activity approximately 200 ms later (Chen and Thompson, 1995). These physiological results, together with the psychophysical findings, indicate that the brain possesses a physiological learning mechanism that makes use of temporal relationships as a learning cue.

Among various approaches to investigating how the motor system adapts to novel environments, arguably the best-studied paradigm is visual disruption using optical prisms (Stratton, 1896; Redding et al., 2005). Experimental paradigms that use wedge-prism displacement of vision are popular in laboratories because they can be conducted in a relatively short time-period compared to dove-prism (i.e., inverted vision) adaptation and can be quantitatively evaluated using definite measures such as learning speed and the magnitude of aftereffects (Held and Gottlieb, 1958; Harris, 1963; Taub and Goldberg, 1973; Hatada et al., 2006).

Recent psychophysical studies have demonstrated that human judgment of temporal simultaneity is not innately fixed but flexibly modifiable after repeated exposure to temporally shifted stimuli in sensory processing within a single modality (Miyazaki et al., 2006) and across

multiple modalities (Fujisaki et al., 2004; Vroomen et al., 2004; Harrar and Harris, 2005; Zampini et al., 2005; Ceux et al., 2006; Hanson et al., 2008; Harrar and Harris, 2008; Keetels and Vroomen, 2008; Boenke et al., 2009; Di Luca et al., 2009; Kennedy et al., 2009; Navarra et al., 2009). Temporal adaptation is not limited to passive sensory processing, but also occurs in active sensorimotor processing. Recalibration of the sensorimotor relationship between self-generated action and temporally modified visual feedback leads to an illusory reversal of their causal relationship (Cunningham et al., 2001; Eagleman and Holcombe, 2002; Stetson et al., 2006; Winter et al., 2008; Heron et al., 2009). Therefore, the point of subjective simultaneity (PSS) can be dissociated from the point of physical simultaneity between motor action and sensory stimuli. By dissociating subjective simultaneity from physical simultaneity, a delay that a participant experiences would be expected to differ from the physical delay. That is, a subjective delay should be reduced or increased relative to a physical delay, to an extent determined by how much the PSS has adapted.

In this study, we tested whether motor adaptation depended on subjective delay or physical delay when participants dissociated subjective and physical timing. These hypotheses are referred to as the “subjective-timing” and “physical-timing” hypotheses, respectively, throughout this paper. In other words, we sought to investigate the functional levels that play important roles in prism adaptation. If prism adaptation depends on subjective delay, the level of prism adaptation would be expected to reside within cognitive time perception and higher motor control systems. Alternatively, if it depends on physical delay, lower, autonomous motor systems would be expected to play a dominant role in prism adaptation. To test these hypotheses, we compared learning speed during adaptation to lateral visual displacement when participants’ subjective simultaneity was dissociated from physical simultaneity. Recent studies evaluating generalization

of temporal adaptation across different multi-sensory pairs have raised questions about whether there is a single clock (Hanson et al., 2008; Heron et al., 2009) or multiple clocks (Miyazaki et al., 2006; Harrar and Harris, 2008) involved in sensory systems. Our study was conducted in accord with these studies, and extended them to question whether the motor system responsible for prism adaptation and the sensory system responsible for temporal order judgment are governed by a single clock or not.

METHODS

Participants

Ten right-handed adults from our institute and a nearby university (age: 18-47; nine male and one female) took part in Experiments 1 and 2, and fifteen right-handed adults (age: 21-49; thirteen male and two female) took part in Experiment 3. We obtained written consent from all the participants. The study was approved by an institutional ethics committee. The participants reported no known neurological history and had normal or corrected-to-normal vision.

Experimental setting

We closely followed the experimental setting described in previous studies of prism adaptation (Kitazawa et al., 1995). We describe the paradigm briefly below for convenience. The experimental setup consisted of a 17-inch CRT (85Hz refresh rate: CV772X, TOTOKU Electric Coop, Tokyo, JAPAN) for presenting visual stimuli, a touch screen on the display that measured pointed locations, a custom-made liquid-crystal shutter for controlling the timing of visual feedback (Takei Coop, Niigata, JAPAN), a button for measuring movement onset time, and a mouse for recording participants' responses (Fig. 1A). The participants sat comfortably in front of the desk and wore goggles that restricted their vision in the central field. Their heads were

stabilized on a chin rest, and the distance between the participants' head and the display was measured and fixed at 30 cm. On the goggles, rightward-displacement prisms (15-diopter) were placed that could be flipped on and off manually, and induced a rightward visual shift of approximately 10.7 cm on the screen. In-house Matlab codes on a Windows-based computer, using the Psychophysics toolbox extensions (Brainard, 1997; Pelli, 1997), were used to present visual stimuli, to record the participants' responses, and to control the timing of opening (full visual feedback) and blocking (no visual feedback) the liquid-crystal shutter. The display location was adjusted with or without prisms so that targets fell into the central visual field of participants (Fig. 1B). The participants wore headphones through which white-noise sound was played to block external sounds (i.e., the sound of fingers hitting the screen) so that they would not notice the timing of touching the screen by listening. We chose 100 ms for the intended delay duration because this value has been shown to be effective in decreasing prism adaptation speed (Kitazawa et al., 1995) and in inducing temporal shift adaptation (Stetson et al., 2006; Heron et al., 2009).

Because this study focused on human timing perception, it was important to verify that the timing of visual feedback was precisely and consistently controlled as we intended. Because of the processing time of the PC and the response time of the liquid-crystal shutter, the presentation of visual feedback inevitably involved a slight additional delay larger than 0-ms (i.e., no delay included in the stimulus-presentation code), both when no delay was intended, and when a 100-ms delay period was intentionally included, as described below. We used a commercial high-speed digital camera (EX-F1, Casio, Japan, maximum 1,200 frames per second) to measure the temporal interval from the moment at which a participant's finger hit the screen to the moment at which visual feedback appeared at the display. The interval was measured when either no delay or a 100-ms delay was imposed between the above two moments by the stimulus

presentation code. The measurement was repeated 30 times for each condition. The mean of the measured delay interval was 36.4 (SD 5.08) ms when a 0-ms delay was intended, and 136.4 (SD 4.67) ms when a 100 ms-delay was intended. Thus, we refer to the two conditions as the “minimum 36-ms delay” (or simply “minimum delay”) and “136-ms delay” conditions to reflect the actual delay times for visual feedback.

Psychophysical experiments

Two psychophysical experiments (Experiments 1 & 2) were conducted with ten participants, and one experiment (Experiment 3) was conducted with fifteen participants. All the experiments used the same experimental setting as described above, shown in Fig. 1A. Experiment 1 (delay adaptation experiment) measured the shift of PSS to examine the degree to which the participants exhibited temporal lag adaptation during prism adaptation. Experiment 2 (prism adaptation experiment) then evaluated how temporal lag adaptation affected the learning rate of prism adaptation under three conditions: (1) minimum-delay (MD), (2) physical-delay (PD), and (3) delay-adapted (DA) conditions, which are described in detail below. Finally, Experiment 3 determined the learning rate using a delay that was reduced by the magnitude of the PSS shift measured in Experiment 1. The condition tested in Experiment 3 was thus referred to as the subjective-delay (SD) condition.

Before the three experiments, the participants underwent training sessions to familiarize themselves with the experimental setting and movement requirements.

General procedures

The participants were required to make a whole upper-limb (right arm) movement in a similar

way in the three experiments. The commonalities are described in Fig. 1C. At the beginning of the experiment, they were instructed to wait for auditory cues (four beeps, three low-frequency tones followed by a high-frequency tone) from the headphones, indicating target onset (a yellow cross, 1 cm × 1 cm). As soon as a target was presented, the participants were asked to respond with their right index finger within a reaction time limit of 200 ms, by releasing the button and making a rapid pointing movement toward the target within a movement time limit of 250 ms. Each target was displayed at a random location (taken from a uniform distribution) in a 4 cm × 4 cm square at the center of display. From the time the participants released the button to the time the participants reached the touch screen, the vision was fully blocked by closing the liquid-crystal shutter. When the finger movement terminated on the touch screen, the blockage of vision was removed by clearing up the shutter, and the participants were allowed to view the target and their finger location. By blocking visual feedback during the movement, the participants were prevented from making any online movement corrections, and could adapt only by using the terminal feedback of the endpoint position. In some trials, an artificial delay was imposed by controlling the timing of shutter opening, for the purpose of either inducing a shift of subjective simultaneity (Experiment 1) or examining the influence of delayed feedback on prism adaptation (Experiments 2 & 3).

In our precursory experiments, a computer cursor was used to indicate the endpoints. However, the learning curves did not exhibit an incremental exponential decay, consistent with a previous report (Norris et al., 2001), and the aftereffects were not significant (Clower and Boussaoud, 2000). As such, we provided a full view of participants' own hands and fingers at the end of the movement. We also observed in preliminary experiments that rather strict constraints on reaction and movement times were necessary for reproducing exponential learning curves (see also

DISCUSSION).

Pointing practice sessions

The purpose of these training sessions was (1) to familiarize the participants to the experimental environment and (2) for the participants to practice responding and moving as quickly as possible while maintaining precise endpoint accuracy. Before proceeding to the experiments, the participants underwent training sessions (30 trials each) until they passed the following criteria. The participants were required to satisfy both the response-time and movement-time limits in no less than 90% of trials in a single training session. Additionally, we required participants to complete at least 50% of trials with movement error (defined as the Euclidean distance between a target and final finger positions) that was no more than 1 cm. The participants proceeded to the PSS and prism adaptation experiments when these two criteria were satisfied.

Experiment 1: Delay-adaptation experiment

The purpose of Experiment 1 was to investigate whether temporal-order judgment (TOJ) adapted in a large-amplitude movement involving full upper-limb movement under conditions of laterally displaced vision. Previous studies reported a shift in PSS between a keyboard press (limited to finger movement of small amplitude) and temporally delayed yet spatially intact visual feedback (Stetson et al., 2006). It is currently unclear whether temporal adaptation occurs in our experimental conditions (full arm movement and displaced vision). Therefore, we asked the participants to judge the temporal order between finger tactile feedback and visual feedback. The timing of visual feedback could be manipulated by a liquid-crystal shutter installed directly in front of participants' faces (Fig. 1A).

A single session consisted of 60 initial delay adaptation trials (without prism) followed by 20 subsequent test trials (with prism). In the initial trials in the baseline condition, visual feedback of touched location on the screen was provided by opening the shutter immediately after the participants touched the screen. In the initial trials of the delay adaptation condition, visual feedback was provided 136 ms after the participants touched the screen. We assessed the effect of delay adaptation using a TOJ task. During the test trials, visual feedback was presented at various times from the movement onset as follows. An average movement duration was computed from the previous five trials, and the timing of visual feedback was randomly determined by adding a Gaussian random number (mean 0 ms, standard deviation 80 ms) to the average movement duration, so visual feedback appeared on the display either before or after a participant touched the screen. The participants were asked to report whether they felt the visual feedback was before or after the moment they touched the screen by pressing the middle (before) or left (after) button of a computer mouse held in their left hands.

Experiment 2: Prism-adaptation experiment after delay adaptation

In the second experiment, the participants completed a total 120 runs of pointing movements, and adapted then de-adapted to laterally displaced vision induced with wedge prisms under the minimum-delay (MD), physical-delay (PD), and delay-adapted (DA) conditions. During 60 initial baseline trials (trials 1-60) without prism displacement, visual feedback was displayed without any intentionally imposed delay (corresponding to an actual delay of 36 ms) in the MD and PD conditions, and with an additional 100 ms delay (corresponding to an actual delay of 136 ms) in the DA condition. Subsequently, during 30 trials (trials 61-90) with laterally displaced vision to which the participants adapted, the induced delay was 36 ms in the MD condition and 136 ms in the PD and DA conditions. Finally, during the last 30 de-adaptation trials (trials 91-120), the 36

ms delay was imposed for the three conditions. These delays are summarized in Table 1. The inter-trial interval was 4 s within the baseline, adaptation, and de-adaptation trial blocks. There were short time intervals (usually less than one minute) immediately before the 61st and 91st trials, in which the experimenter flipped on and off the prism on the goggles and adjusted the CRT position (Fig. 1B). During these breaks, the participants were asked to close their eyes. All the participants completed two runs of each of the three conditions, resulting in six sessions per participant. The presentation order of the conditions was randomized from participant to participant, and a break of several minutes was taken between sessions.

Experiment 3: Prism-adaptation experiment with PSS-shift-reduced delay

The purpose of the third experiment was to explicitly evaluate the effects of a physical delay that was matched to the amount of subjective delay exhibited on the learning rate of prism adaptation. Participants underwent a prism adaptation experiment that was same as in the PD condition of Experiment 2 with one exception: the delay in adaptation trials was reduced by the magnitude of the PSS shift determined in Experiment 1 (bottom row in Table 1). This condition was referred to as the subjective delay (SD) condition. By comparing the learning coefficients measured in the SD and DA conditions, it was possible to evaluate the degree to which the learning rate was determined by the subjective delay.

Data Analysis

All experimental data was analyzed using Matlab and its Statistical Toolbox (MathWorks, MA) and JMP (SAS Institute Inc., NC).

Experiment 1: Delay adaptation experiment

For the delay adaptation experiment, the degree to which the participants shifted their PSS was evaluated according to Stetson et al. (2006). First, feedback timing (i.e., the time of opening shutter from the time of participants' touching the screen) was binned into a 60 ms interval between -200 to 200 ms. In each bin we computed the probability that each participant judged visual feedback to have occurred after the movement was completed. For example, in the i -th bin, if a participant reported n_i times out of N_i occurrences that the visual feedback occurred after the screen touch, then the probability of judging "after" was evaluated as n_i/N_i . Next, a sigmoid function,

$$\text{Prob}[\text{feedback judged after touch}] = \frac{1}{1 + \exp\left(-\frac{t - t_0}{b}\right)},$$

was fitted to obtain a psychometric curve using a Matlab *glmfit* function. t is the time of visual feedback measured from the time of touching, and t_0 and b are the intercept and the slope, respectively. In addition to individual psychometric curves, a group psychometric curve was similarly computed by summing up all participants' responses.

Generally speaking, two adaptive consequences can be caused by repeated exposure to asynchronous stimuli (Hanson et al., 2008). One possibility is the broadening of the temporal window of simultaneity between stimuli so that temporally asynchronous stimuli are perceived as simultaneous. This type of adaptation would manifest as a shallower psychometric curve (i.e., larger slope b) with a larger just noticeable difference (JND). Another possibility is a shift in the point of subjective simultaneity (PSS) between exposed stimuli so that temporal asynchrony is subjectively cancelled. In this case, the intercept of a psychometric curve (t_0) would be displaced according to the amount of PSS shift. Therefore, we examined whether the participants broadened the temporal time window or shifted the PSS by investigating the slope and intercept of

psychometric curves.

Experiments 2 & 3: Prism adaptation experiment

There are at least two methods for quantifying learning speed in prism adaptation experiments; a state-space model approach (Baddeley et al., 2003; Cheng and Sabes, 2006) and a discrete-model approach (Kitazawa et al., 1995; Yin and Kitazawa, 2001). We used the latter method, so that our findings would be comparable with Kitazawa's results. The learning-speed coefficients, k , were computed for learning curves according to the methods of Kitazawa et al. (1995), and were statistically compared between the conditions. First, the learning coefficient k is defined as a portion of an error in previous trial that reduces an error in current trial;

$$\varepsilon_n = \varepsilon_n - k\varepsilon_{n-1}.$$

Here the subscript n denotes the trial number from adaptation onset, and ε_n denotes the movement error at n -th trial. Then, recursively applying this equation we obtain

$$\varepsilon_n - \varepsilon_1 = k \sum_{i=1}^{n-1} \varepsilon_i.$$

Therefore, k can be computed as a slope of a line connecting the origin and $\left(\sum_{i=1}^{n-1} \varepsilon_i, \varepsilon_n - \varepsilon_1 \right)$.

Practically, we have such $(n-1)$ points $\left(\sum_{i=1}^{n-1} \varepsilon_i, \varepsilon_n - \varepsilon_1 \right)$ (in our case 29 points for each

participant), and the coefficient k and the intercept were estimated using an ordinary least square fitting:

$$\sum_{n=2}^{30} \left(\varepsilon_n - \varepsilon_1 - k \sum_{i=1}^{n-1} \varepsilon_i \right)^2$$

The k 's obtained in the four conditions (denoted as k_{MD} , k_{PD} , k_{DA} , and k_{SD} respectively) were

statistically compared to test whether they were different according to the conditions.

Predictions of the physical-timing and subjective-timing hypotheses

Before we conducted the prism adaptation experiment, we had two hypotheses about the timing of feedback that predominantly contributed to the learning speed of prism adaptation. If participants adapted fully to the imposed delay of 100 ms, the PSS would be expected to shift by 100 ms. Thus, the subjective delay of visual feedback would be the same as that in the MD condition, whereas the physical delay would remain at 136 ms. One hypothesis was that the rate of prism adaptation would depend mostly on the simultaneity that participants subjectively reported (referred to as the subjective-timing hypothesis). According to this prediction, the learning curve in the DA condition would be expected to overlap with that in the MD condition (Fig. 2A) if the PSS shifted the full extent of the imposed delay (100 ms). The other hypothesis was that the physical simultaneity determines the rate of prism adaptation (referred to as the physical-timing hypothesis). This hypothesis predicts that the learning curve in the DA condition should overlap with the PD condition (Fig. 2B).

Previous studies have shown that participants can partially shift their PSS in response to an imposed delay (Stetson et al., 2006; Winter et al., 2008; Heron et al., 2009). In that case, a subjective delay does not become zero even after intensive delay adaptation, and delay adaptation should subjectively reduce physical delay only by the amount of the PSS shift. Therefore, the learning rate in the DA condition should be compared with that in the PD and SD conditions. The subjective-timing hypothesis predicts comparable learning rates in the DA and SD condition. In contrast, the physical-timing hypothesis predicts comparable learning rates in the DA and PD conditions. These predictions were explicitly tested in Experiments 2 and 3.

RESULTS

Before the three experiments, the participants were required to complete training sessions until the two performance criteria described in the method were satisfied. Most participants reported that they felt these criteria to be rather challenging initially; after 6 - 24 training sessions participants generally reported that they felt much more comfortable with the task after training. The practice session usually took 30 - 120 minutes including breaks.

PSS shift occurring in whole limb movement under prism displacement

In Experiment 1, we quantified, as a function of the time difference between the participants' screen touch and visual feedback, the probability that the participants reported that visual feedback occurred post movement (open and filled circles in Fig. 3A). The probability was fit by a sigmoid function (broken and solid lines in Fig. 3A). The post-adaptation curves clearly shifted toward rightward compared to the pre-adaptation curves. The shift was evaluated as an intercept (t_0 : see METHODS) of the post-adaptation curve measured from an intercept of the pre-adaptation curve. The evaluated shifts were 40.1 (SD: 10.1) ms averaged across subjects. This was significantly larger than zero according to a one-sided t-test ($t(9) = 5.58$; $P = 0.0002$). This indicates that the participants' PSS adapted to the repeated, delayed feedback in the whole limb movements. We also quantified the slopes (b) of psychometric curves, finding that the slope-value averaged across participants was 42.9 (SD 16.4) ms for the pre-adaptation curve and 40.6 (SD 10.4) ms for the post-adaptation curve. There was no significant difference in slope values between the curves ($t(9) = 0.38$). The group averaged psychometric curves are shown in Fig. 3B. The slopes were similar, and only the intercepts were shifted, indicating that persistent delayed feedback shifted the PSS but did not broaden the JND in temporal perception. The

subjective delay caused by the temporal adaptation was thus approximately 96 ms (physical delay (136 ms) – shift of PSS (40 ms)).

Delay adaptation had no effect on learning rate

5 In Experiment 2, we examined prism adaptation under the three different visual-feedback timing conditions (i.e. the minimum-delay (MD), physical-delay (PD), and delay-adapted (DA) conditions; see METHODS section and Table 1). We imposed the rather demanding time constraints for reaction and movement times so that the participants did not use any cognitive or strategic methods for correcting endpoint errors (see DISCUSSION). During the baseline,
10 adaptation, and de-adaptation trials, the reaction and movement times were relatively constant (Figs. 4A & B). There was a slight increase of reaction time in initial trials of adaptation and deadaptation blocks (the 61st and 91st trials in Fig. 4A). This may have been caused by short time intervals in which the experimenter flipped the prism on the goggles on and off. Vertical errors were close to zero in the three blocks when they were averaged across trials, conditions and
15 subjects (baseline: -0.15 ± 1.08 , adaptation: -0.20 ± 1.35 , and de-adaptation: 0.04 ± 1.22 cm; a positive or negative value indicates an upper or lower error relative to the target). We conducted a two-way (block by condition) repeated-measures ANOVA on the vertical errors but could not find a significant effect of block ($F(2,18) = 1.76$) or condition ($F(2,18) = 0.13$). This indicates that the horizontal displacement caused by the prism had no effect on the perpendicular direction.

20 Learning curves of horizontal errors in the three conditions exhibited typical exponential decay functions (Fig. 5A: MD in blue, PD in black, and DA in red). The endpoint errors in the initial trial of adaptation (61st trial) were significantly smaller (8.1 ± 2.3 cm) than the visual displacement imposed by the prism (10.7cm), as reported in a previous work (Redding and Wallace, 2003).

There were no significant differences between the initial errors in the three conditions (8.4 ± 1.6 for MD, 8.0 ± 2.4 for PD, and 8.0 ± 2.7 cm for DA; $p = 0.80$, $F(2,57) = 0.23$, one-way ANOVA). First, we attempted to replicate Kitazawa's result that an artificially induced delay in visual feedback leads to a slower adaptation speed of prism adaptation. We found that learning speed was significantly slowed when the feedback delay was introduced in the PD condition (black curve in Fig. 5A) compared when no intentional delay was imposed (blue curve in Fig. 5A), consistent with Kitazawa's findings. The learning coefficients in the MD and PD conditions were 9.0 ± 7.0 % and 6.3 ± 4.6 %, respectively (left and middle box plots in Fig. 5B).

The learning curve in the DA condition (red curve in Fig. 5A) largely overlapped with that in the PD condition but not in the MD condition. In accord with this observation, the learning coefficients in the DA condition (right box plot in Fig. 5B, 5.9 ± 4.6 %) were significantly smaller than those in the MD condition but not significantly different from those in the PD condition (at $P < 0.05$ level corrected for multiple comparisons by Tukey's test). Therefore, for the DA condition, the delay adaptation in the baseline trials had no effect on the learning coefficients during adaptation trials.

Subjective delay could not explain the reduced learning rate in delay-adapted condition

The delay adaptation experiment indicated that subjective simultaneity shifted by approximately 40 ms, thereby reducing the subjective delay from the actual delay of 136 ms to only 96 ms. Learning rate was previously reported to rapidly decrease up to a feedback delay of 50 ms, and gradually decrease with a delay greater than 50 ms (see Figure 5C of Kitazawa et al., 1995). Thus, learning rates with 96-ms and 136-ms delay might not differ enough to confirm or disconfirm either of the two hypotheses. The results of Experiment 2, together with the findings of Kitazawa

et al. (1995), could not decisively determine whether the decreased learning rate in the DA condition was attributable to the physical delay (136 ms) or the subjective delay (96 ms).

In Experiment 3, participants adapted to prism displacement with a physical delay that was matched to the subjective delay of 96 ms (referred to as the subjective-delay (SD) condition). We found, in our experimental setting, that the learning coefficients in the SD condition were significantly larger than those in the DA condition, according to a t -test ($t(48) = 2.25, P < 0.05$; Fig. 6). Therefore, the reduced learning rate in the DA condition could not be attributed to the subjective delay of 96 ms, excluding the subjective-timing hypothesis. To check whether sampling bias between subject groups in Experiments 2 and 3 affected this finding, we compared learning coefficients in the SD condition in Experiment 3 with those in the MD condition in Experiment 2. There was no significant difference between them ($t(48) = 0.60$), and thus unlikely sampling bias affected the result.

DISCUSSION

This study tested how subjectively modifying the timing between sensorimotor events influenced the learning of a novel visuomotor environment. The results revealed two major findings. First, in Experiment 1 (delay-adaptation experiment), most participants showed a dissociation between their subjective timing and the physical timing, even in conditions involving a whole-limb pointing response with displaced vision. The extent of temporal adaptation we observed was not complete. In this partial adaptation, a shift of the PSS of approximately 40 ms was observed after adapting to conditions of feedback delayed by 100 ms, consistent with a previous result. Therefore, a subjective delay was reduced to approximately 96 ms by the PSS

shift of 40 ms when the physical delay in visual feedback was actually 136 ms. Experiment 2 (prism adaptation experiment) revealed that the learning rate in the delay-adapted condition was significantly slower than in the minimum-delay condition, but was not different from in the physical-delay condition. The result obtained in Experiment 3 demonstrated that the decreased learning rate in the delay-adapted condition could not be attributed to the subjective delay of 96 ms, thereby disconfirming the subjective-timing hypothesis. In summary, we concluded that learning speed in prism adaptation depended on the physical time interval between touching and visual feedback, but was not affected by subjective temporal perception.

Recalibration and realignment processes in prism adaptation

Two possible adaptive processes for correcting endpoint errors have been proposed in previous reports (Redding and Wallace, 2001; Mazzoni and Krakauer, 2006; Michel et al., 2007). One is a realignment process (also referred to as an explicit or strategic process) in which a participant responds to an illusory target that is located opposite to the prism displacement. This requires explicit knowledge about the size and direction of displacement, and planning to compensate for the displacement. An alternative possibility is that a recalibration process (also referred to as an implicit or automatic process) is involved, correcting movements incrementally without any explicit knowledge about how a movement error was caused (Kagerer et al., 1997).

In our experiments, we instructed the participants to react and move as rapidly as they could within stringent time constraints, providing insufficient extra time for developing a realignment process between the target and movement onsets. Our experiments thus predominantly targeted a recalibration process of prism adaptation. The results thus indicate that such a recalibration process depends mostly on physical timing but not subjective timing. This finding is in accord

with the absence of subjective awareness involved in recalibration processes.

Neural sites of prism adaptation and temporal perception

Functional neuroimaging and electrophysiological studies have suggested a number of cortical and subcortical areas to be involved in prism adaptation, including the cerebellum (Luaute et al., 2009), the ventral premotor cortex (Kurata and Hoshi, 1999), and the posterior parietal cortex (PPC; Clower et al., 1996). Pisella et al. (2004) proposed that explicit and strategic realignment is linked to PPC activity, while implicit and automatic recalibration is linked to the cerebellum. In contrast, Stetson et al. (2006) reported activation related to the temporal reversal illusion in the anterior cingulate cortex and the medial frontal cortex. Therefore, prism adaptation and this temporal illusion do not appear to overlap in terms of neural substrates, in accord with our conclusion that the shift in PSS had no influence on the learning rate in prism adaptation.

Prism adaptation under reversed cause-effect relationship

Arguably the most intriguing aspect of temporal adaptation is that our subjective timing of cause and effect can be illusorily reversed (Cunningham et al., 2001; Stetson et al., 2006). According to these studies, for example, after being exposed repeatedly to 100 ms delayed visual feedback of a button press, the sudden removal of the delay can lead to the impression that visual feedback occurs in advance of the button press. Therefore, the subjective causality can be broken down in some cases. Whether it is possible to adapt to prism displacement even when visual error feedback is not perceived to be a result of self-movements is currently unclear. We performed an exploratory experiment with six participants in which an intentional 100-ms feedback delay was imposed during 60 baseline trials, with no intentional delay during subsequent 30 prism adaptation trials. Participants exhibited typical exponential learning curves, and their learning

speed was similar to that in a no-delay condition. This result was in accord with the main finding of the current study, that subjective timing did not influence the learning speed of prism adaptation or the automatic processes underlying movement recalibration.

Table 1: Actual feedback delay used for the minimum-delay, physical-delay, delay-adapted, and subjective-delay conditions.

Condition	Baseline (60 trials)	Adaptation (30 trials)	De-adaptation (30 trials)
Minimum Delay (MD)	36 ms	36 ms	36 ms
Physical Delay (PD)	36 ms	136 ms	36 ms
Delay Adapted (DA)	136 ms	136 ms	36 ms
Subjective Delay (SD)	36 ms	96 ms	36 ms

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Figure legends

Figure 1

(A) A schematic of experimental setting used in this study, (B) display locations (rectangles) with and without prism, and (C) time flow of a typical, single trial.

Figure 2

Expected learning curves after full adaptation to temporal delay when prism adaptation depends on (A) subjective timing or (B) physical timing. MD: Minimum delay, PD: Physical delay, DA: Delay adapted, SD: Subjective delay.

Figure 3

(A) Psychometric curves from all participants and (B) group-average psychometric curves for the control (broken lines) and delay-adapted (solid lines) conditions. The circles along the curves (open and filled circles for the control and delay-adapted conditions, respectively) indicate how many reaches were performed in individual time bins (the circles in the right-bottom corner represent 20 reaches).

Figure 4

(A) Reaction and (B) movement times during the prism experiment. Blue, black and red solid lines with markers denote mean values for the minimum-delay, physical-delay and delay-adapted conditions, respectively. Thin broken lines indicate standard deviations. Gray shaded areas indicate prism-adaptation trials (61-90).

Figure 5

(A) Average learning curves from ten participants obtained in the minimum-delay (blue), the physical-delay (black), and the delay-adapted (red) conditions. Thin broken lines indicate standard deviations. There was no systematic change in the baseline trials, hence only the last thirty trial errors are shown to demonstrate how variable the movements were when no visual displacement was imposed. (B) Learning coefficients in the three conditions. In the box plots, horizontal black lines indicate median values, and the bottom and top of boxes indicate 25th and 75th percentiles. The whiskers cover 9th and 91st percentiles. *: $P < 0.05$, N.S.: not significant according to Tukey's test.

Figure 6

Box plots of learning coefficients for the delay-adapted and subjective-delay conditions. The left box plot for coefficients in the delay-adapted condition is the same as in Figure 5B, and is included for comparison. *: $P < 0.05$ according to t -test.

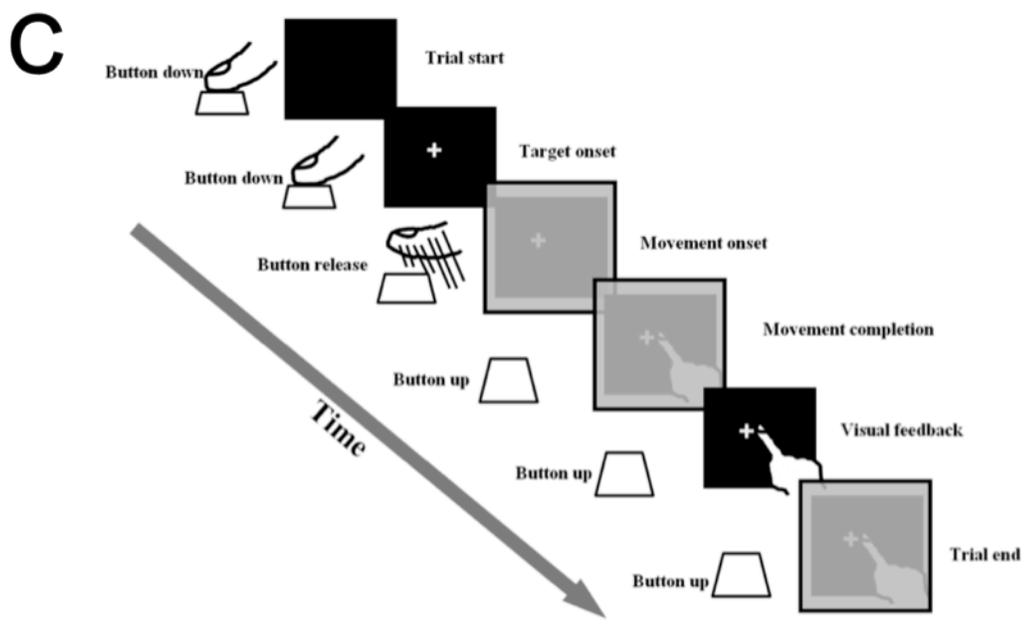
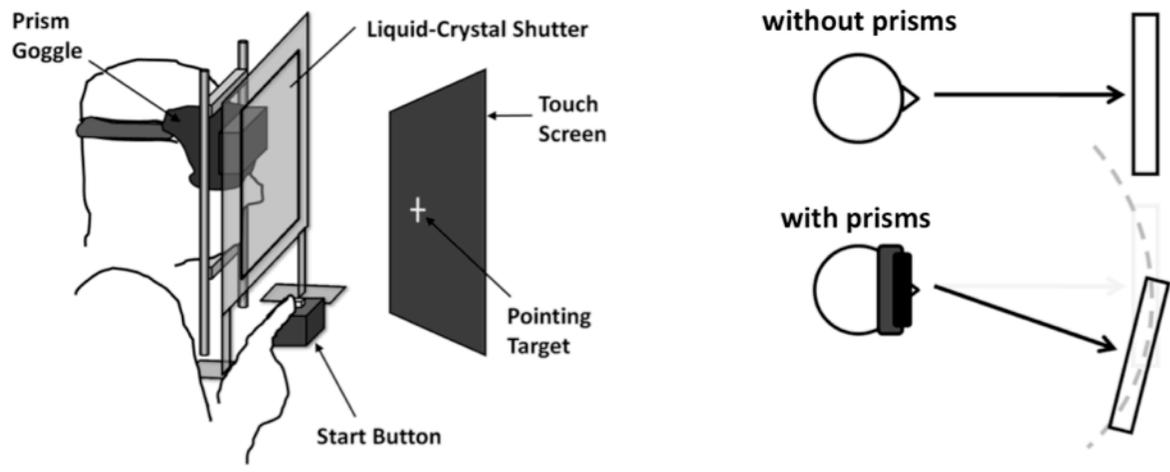


Figure 1

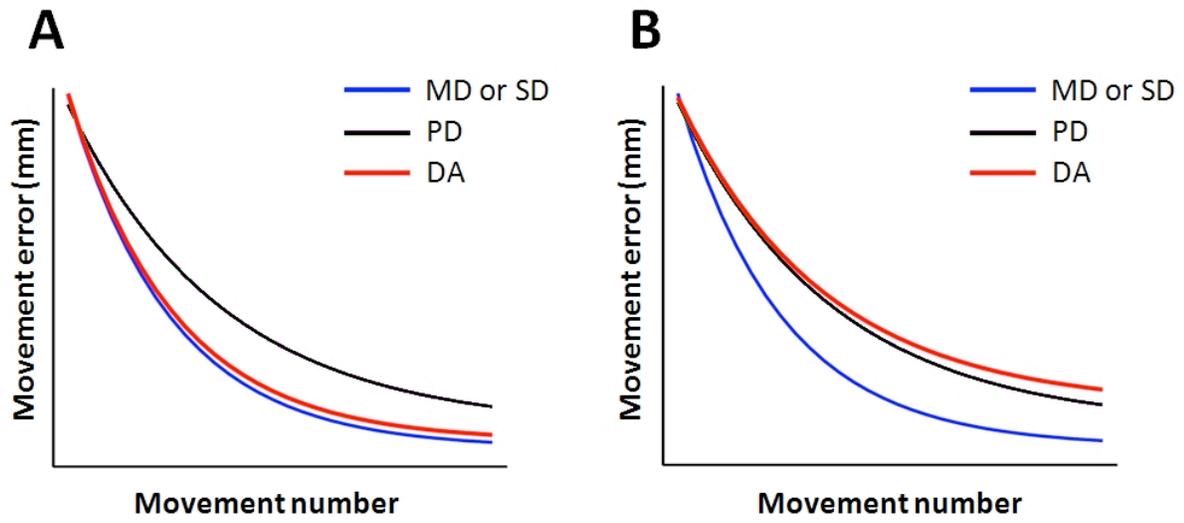


Figure 2

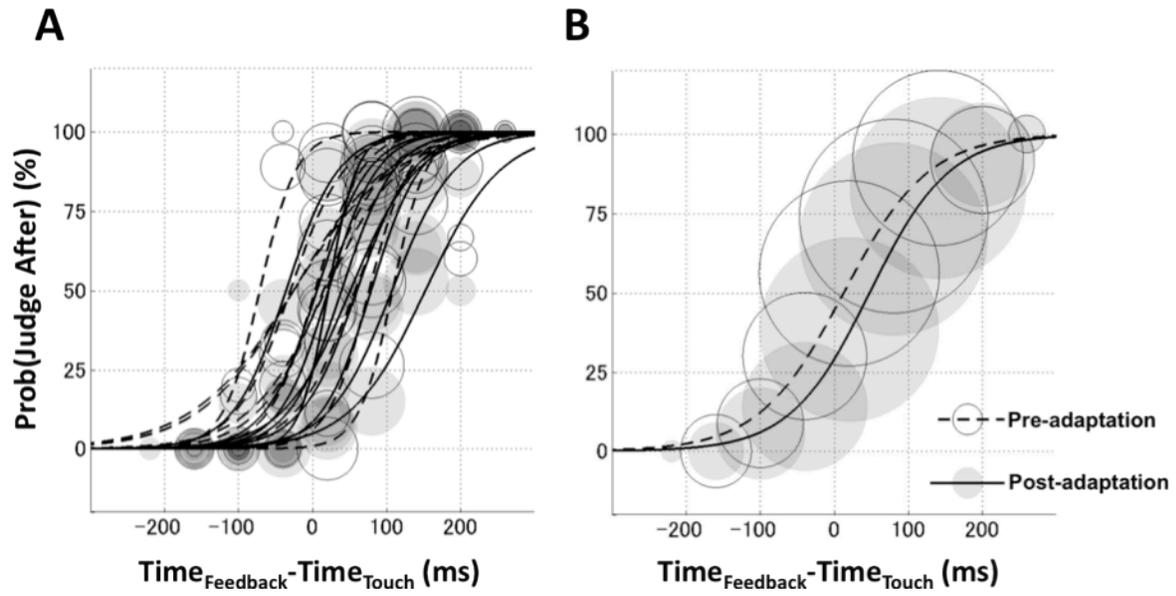


Figure 3

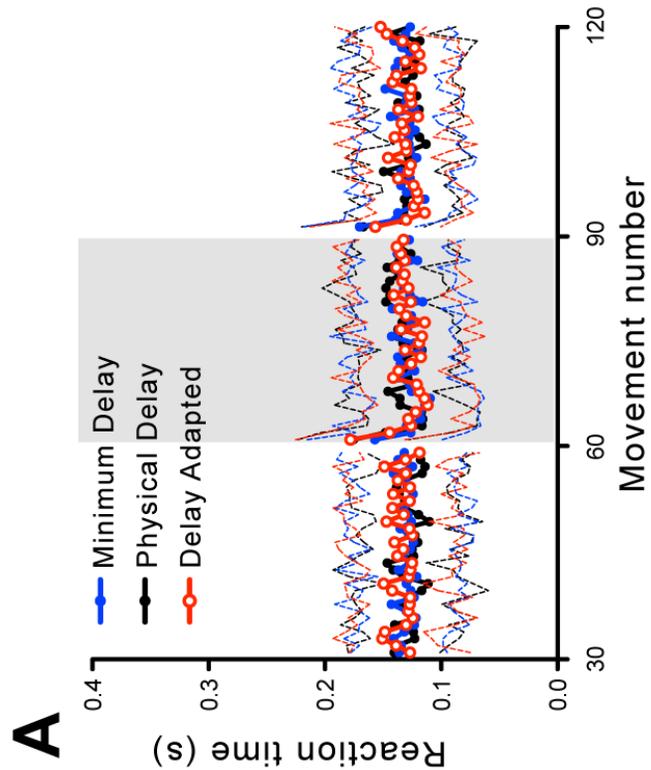
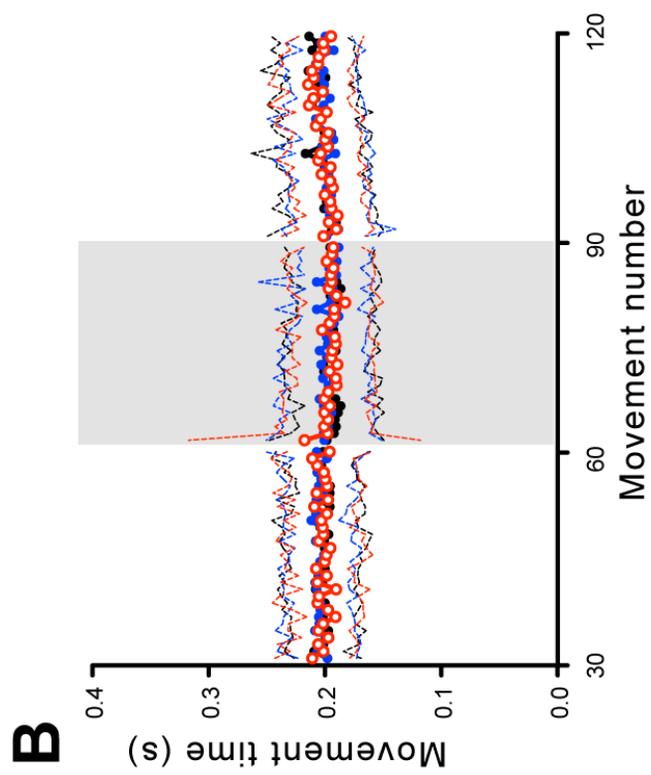


Figure 4

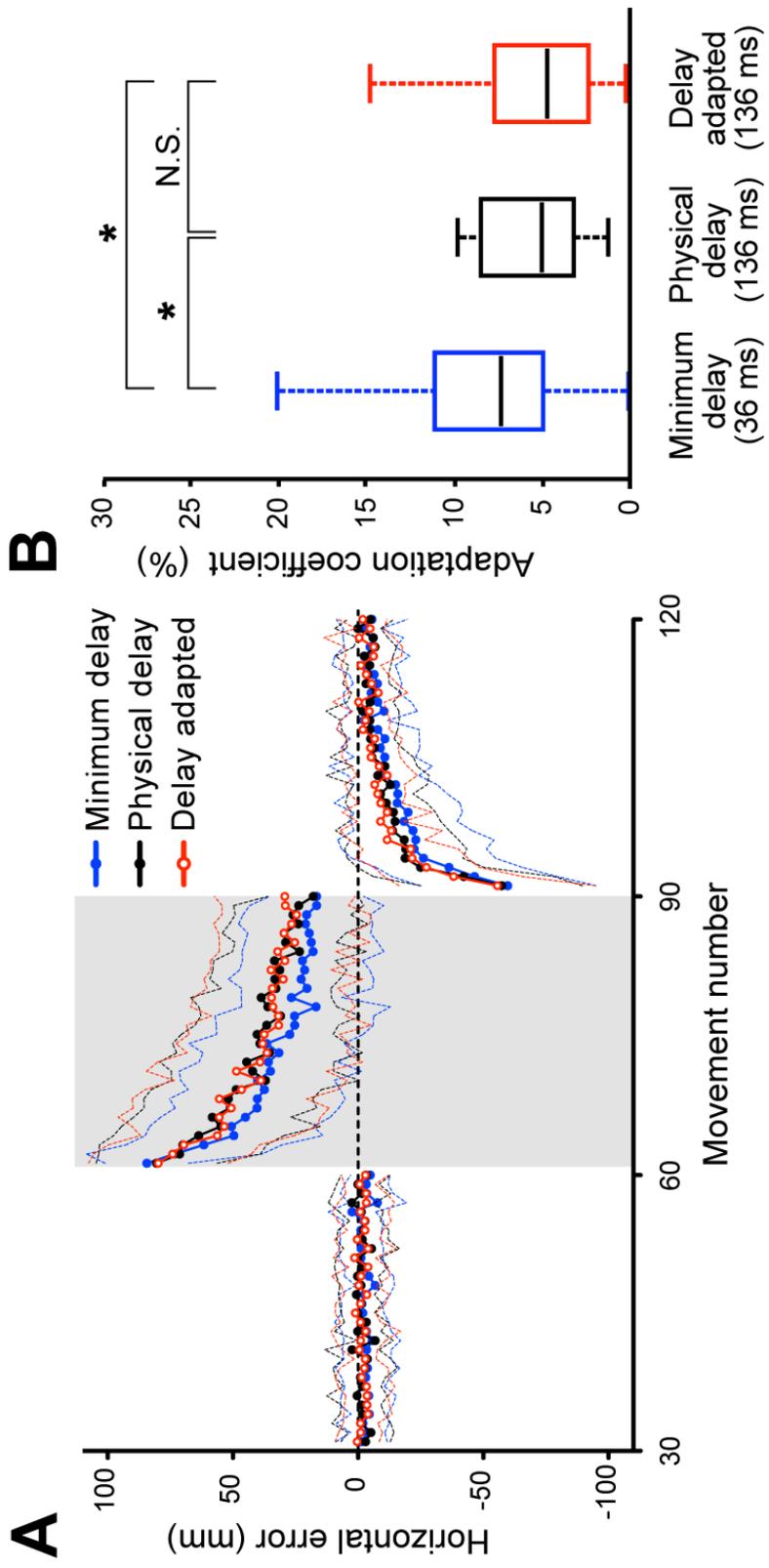


Figure 5

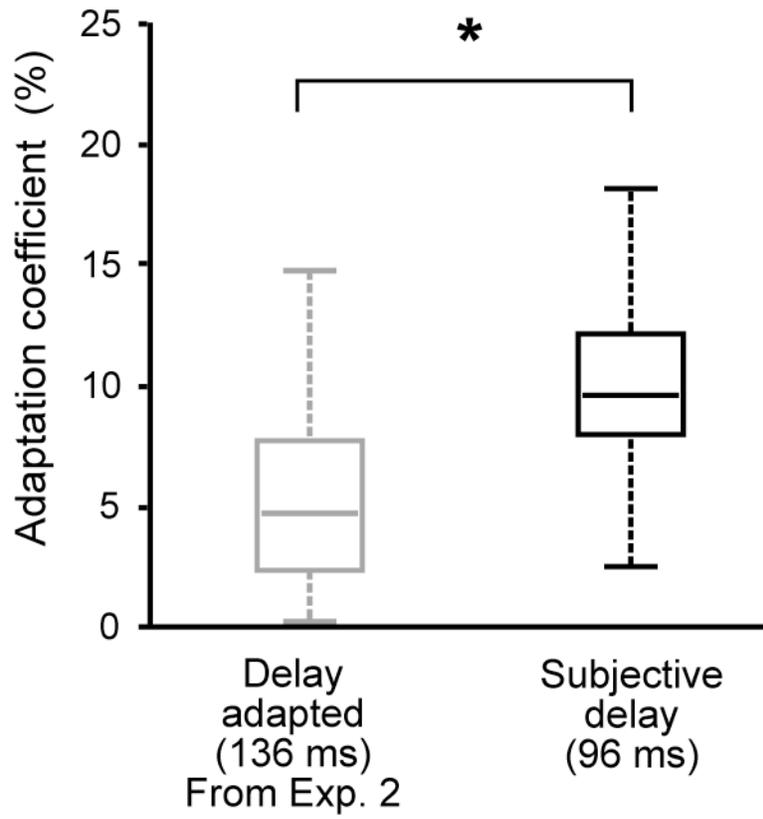


Figure 6