Enhancements of the offline improvement in human motor skill

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Summary

People acquire a lot of motor skills in life, and acquired skills are frequently used in everyday. Many people probably hope to learn the skills as fast and easy as possible. Motor skills are initially acquired across the training, and then are sophisticated over time. The term of consolidation is described as the process that converts newly acquired fragile memory into more robust and stable forms (Robertson et al., 2004). Consolidation has a critical role in long-term skill retention (Karni et al., 1995; Brashers-Krug et al., 1996). Specifically, for procedural skill, offline improvement refers to the skill improvements that occur between practice sessions without physical practices, and is thought to be a form of skill consolidation (Walker et al., 2002, 2003; Fishcer et al., 2002). Therefore, the goal of current project was to clarify the enhancement factors for the offline performance improvements in human motor skill. To accomplish this goal, I focused sleep and social rewards as potential enhancing factors, and conducted two independent behavioral studies to determine the effect of these factors in offline skill improvements.

First, sleep is necessary for certain skill consolidation in adults (Walker, 2005; Stickgold, 2005; Diekelmann & Born, 2010). On the other hand, it remains debatable whether skill consolidation benefits from sleep in children as well as in adults (Fisher et al., 2007; Wilhelm et al., 2009). In Study 1, I focused on the offline improvement, which is one type of skill consolidation and has been known to depend on the sleep in adults. Here, I investigated whether in children, sleep duration after motor training was correlated with the rate of offline improvement. On first day, 9 (n = 14) and 11 years-old children (n = 10) trained a sequential finger tapping skill (Walker et al., 2002, 2003). Their parents observed and recorded their children's sleep duration after this training. On the next day, to assess the rate of offline improvement, all children performed a surprise retest session for previously trained sequence. My present data indicated that in both 9 and 11 years-old children, skill performance significantly improved at first retest session relative to that at the end of training on previous day ($p < .0001$), confirming that offline performance improvement took place, and the rate of this improvement was significantly correlated with the sleep duration during the night after the training ($\beta = 0.60$, $p < .01$). Consequently, I conclude that in children as well as adults, sleep is associated with a type of skill consolidation.

Second, praise, a social reward, is thought to boost motor skill learning by increasing motivation, which leads to increased practice (Catano, 1975; Henderlong & Lepper, 2002). However, the effect of praise on consolidation is unknown. In Study 2, I tested the hypothesis that praise following motor training directly facilitates skill consolidation. Forty-eight healthy participants were trained on a sequential finger-tapping task. Immediately after training, participants were divided into three groups according to whether they received praise for their own training performance (Self group, $n = 17$), praise for another participant's performance (Other group, $n = 15$), or no praise (No-praise group, $n = 16$). Participants who received praise for their own performance showed a significantly higher rate of offline improvement (19.95 ± 1.85%) relative to other participants (Other: 13.14 ± 1.82%, $p < .05$; No-praise: 13.14 ± 1.82%, $p < .05$) when performing a surprise recall test of the learned sequence. On the other hand, the average performance of the novel sequence and randomly-ordered tapping did not differ between the three experimental groups ($ps > 0.60$). These results are the first to indicate that praise-related improvements in motor skill memory are not due to a feedback-incentive mechanism, but instead involve direct effects on the offline consolidation process.

In conclusion, I found two important factors that benefit the skill consolidation. In Study 1, post-training sleep durations were positively correlated to the rate of offline performance improvement in children, suggesting that sleep is the important in children as well as in adults. In Study 2, I found that social rewards directly enhance skill consolidation in humans, suggesting that they have a novel functional effect on the human motor memory system. The current general conclusion is that praise for skill performance and subsequent nocturnal sleep could enhance the rate of offline skill consolidation in at least one type of motor skill such as sequential finger-tapping. These present findings might contribute to develop protocols to improve motor skills in educational and rehabilitative contexts.

Introduction

In real life, people use a lot of skills including writing, typing, sports, and musical instruments. Most people might hope to mastery a lot of skills as fast and easy as possible. Motor skill memory is first encoded online in a fragile form during practice and then converted into a stable form by offline consolidation, which is the behavioral stage critical for successful skill formation (Karni et al., 1995; Brashers-Krug et al., 1996). Here, I focused on two potential contributing factors to enhance the offline consolidation in human motor skill.

One factor is sleep after the skill acquisition. In healthy adults, there are the mounting evidences showing that post-training sleep benefits the certain type of skill consolidation such as sequential finger-tapping movements (Walker et al., 2002; Fischer et al., 2002; Debas et al., 2010) and visual discrimination (Karni et al., 1994; Stickgold et al., 2000). Moreover, the degree of skill consolidation is associated with the total sleep duration (Stickgold et al., 2000) and the specific sleep architectures such as non-REM 2 sleep (Walker et al., 2002; Nishida & Walker, 2007) and sleep spindles

(Nishida & Walker, 2007; Morin et al., 2008; Barakat et al., 2011). On the other hand, despite children train a lot of skill in everyday and have longer sleep durations relative to adults (Largo et al., 2001), there is no evidence to indicate the effect of sleep for the skill consolidation in children. Previous behavioral evidences showed that over 9-year old children exhibited the significant offline performance improvements at 24-hour after skill training (Dorfberger et al., 2007, 2009). Therefore, in present project, I investigated the hypothesis whether longer sleep durations facilitate the degree of offline performance improvements, which is a type of skill consolidation, in elementary school children or not.

Another factor is praise for own skill performance. In real-life skill acquisition, people generally believe that praise for good performance results in further skill improvements. Behavioral evidence indicates that social rewards such as praise accelerate performance during training, possibly via an information feedback-incentive mechanism (Adamas, 1972; Catano, 1975). However, the effects of praise on skill consolidation are not known. The process of skill consolidation is based on plastic changes in the cortico-striatal loop (Doyon et al., 2003; Penhune et al., 2002; Debas et al., 2010), which relies on enhanced dopamine transmission (Calabresi et al., 2007). A recent human neuroimaging study demonstrated that praise activates reward-related areas of the brain, specifically the ventral striatum (Izuma et al., 2008), which is mainly involved in dopamine transmission (Zald et al., 2004). These data led me to hypothesize that praise influences the skill consolidation process directly, as opposed to indirectly through motivating further practice.

The goal of current project was to clarify the potential factors enhancing the offline skill consolidation. Thus, I performed two independent behavioral studies to investigate above-mentioned hypotheses. In Study 1, I investigated whether post-training sleep durations were positively correlated with the degree of offline improvements in 9 and 11 year-old children. In Study 2, I determined the effect of praise for own skill performance in the offline skill consolidation. Accomplishment of present goal might contribute to develop the novel educational and rehabilitational programs, as well as to further understanding the skill consolidation process.

Study 1

Sleep in children facilitates the offline improvement in motor skill

3.1 Introduction

Newly acquired skills become more robust, stable states over time (consolidation; Karni et al., 1993, 1995; Brashers-Krug, 1996; Robertson et al., 2004). Offline improvement refers to the skill improvements that occur between practice sessions without physical practices, and is thought to be a form of skill consolidation. It is well known that sleep has a most benefit to the offline improvement in skill consolidation in healthy adult human (Stickgold et al., 2000; Walker et al., 2002, 2003; Fischer et al., 2002). Moreover, the rate of offline improvement is positively correlated with the total duration of sleep (Stickgold et al., 2000) or with the percentage of specific sleep stage, specifically non-rapid eye movement sleep stage 2 (NREM stage 2; Walker et al., 2002; Nishida & Walker, 2007).

As well as adults, previous studies have shown that children exhibit robust offline improvement in motor sequential learning (Dorfberger et al., 2007, 2009).

However, there are several evidences indicating that offline improvement in children did not required for the sleep, suggesting that children's ability for skill consolidation was different with the adults' one (Fischer et al., 2007; Prehn-Kristensen et al., 2009; Wilhelm et al., 2008). On the other hands, these studies had differences in response to the adapted task and children's ages. Therefore, the purpose of this study was to examine the relationship between sleep and skill consolidation with explicit considerations of children's age and motor-training task. Specifically, the present study firstly investigated the hypothesis that sleep duration after motor sequential training was positively correlated with the rate of offline improvement in 9 and 11 year-old children that exhibited robust offline improvement (Dorfberger et al., 2009, 2012), using the sequential finger-tapping task repeatedly reported sleep-dependent offline improvement in adults (Walker et al., 2002, 2003; Fischer et al., 2002).

To complete this purpose, 9 and 11 year-old children participated in this study for two consecutive days. All children were trained in the modified version of sequential finger-tapping task on day 1 (LRN1; Walker et al., 2002, 2003). After 24-h retention interval including sleep, all children performed the retest of the trained sequence on day 1 (LRN2). Their sleep duration was observed with their parents. In present study, the offline improvement was defined by the percent improvements from LRN1 to LRN2. Here, based on the previous findings in healthy adult study (Karni & Sagi, 2003; Stickgold et al., 2000; Walker et al., 2002, 2003; Fischer et al., 2002), we hypothesized as following: (1) more than 9 year-old children exhibited the significant improvement after 24-h intervals including sleep (Stickgold et al., 2000; Walker et al., 2002; Fischer et al., 2002); (2) the rate of offline improvement was positively correlated with the sleep duration during the night after motor training (Stickgold et al., 2000; Walker et al., 2002).

2.2 Materials and Methods

Participants

Twenty-five children (14 male and 11 females, mean [M] ± standard deviation [SD] = 9.48 ± 1.16 years) participated in this study. According to Edinburgh's Laterality Quatient (LQ), one female was excluded from analyses (LQ = -1.00). Thus, data from 24 right-handed children (14 male and 10 females; M ± SD = 9.42 ± 1.14 years; Edinburgh's LQ, M ± SD = 0.89 ± 0.23) were used for analysis. Participants came to the laboratory on two subsequent days (9 year-old, n = 14; 11 year-old, n = 10). None of participants had a history of neurological, psychiatric, or sleep disorders. The experiment approved by the institutional ethics committee, and informed parental consent was obtained.

Experimental procedure

All participants trained on a modified version of sequential finger-tapping task on day 1. The original version of sequential finger tapping task required participants to press four numeric keys on a standard computer keyboard repeatedly with the fingers of their non-dominant (left) hand as quickly and as accurately as possible for 30-s periods (for details, see Walker et al., 2002, 2003). Given that finger-tapping speed depends on age (Largo et al., 2001), here, the modified version of this task required children to press three keys with the three fingers: index, middle, and ring finger. A white asterisk appeared on a computer monitor at one of three possible positions within an equally spaced horizontal array. Each of the three positions corresponded to one of the three buttons on a numeric keyboard. The stimuli were presented repeatedly for 30 s in the sequence used in the task. On day 1, participants trained on sequence A (LRN1; "3-1-2-1-3"). After the training, all participants received visual feedback about their training performance (for example, their learning curve). On the following day, all participants performed a retest of the trained sequence (LRN2).

Finger tapping performance was evaluated by the number of correctly tapped sequences per 30-s trial. The offline improvement following a night of sleep was defined as the percent increase in mean performance from the last three trials during training (LRN1) on day 1 compared with the first three retest trials (LRN2) on day 2 (Walker et al., 2002; Nishida & Walker, 2007; Debas et al., 2009). Training on day 1 consisted of twelve 30-s trials with 30-s rest periods between trials, whereas the retest on day 2 consisted of five trials with the same rest interval.

Sleep duration and additional ratings

To examine the effect of sleep duration on the offline improvements in motor skill, participants' parents were asked to observe and report the time that their children went to bed on the nights before and after training, and the time that they woke up on the training and retest mornings (Stickgold et al., 2000).

It was possible that participants' subjective states during training or retest might influence their performance. Thus, at the end of the training and retest periods, all participants completed questionnaires about their subjective ratings of alertness (1 = not at all, 10 = very drowsy), concentration (1 = not at all, 10 = very concentrated), and fatigue (1 = high level of fatigue, 10 = no fatigue) during training and retest using a ten-point scale.

Data analysis

Statistical analyses were based on the general linear model using analyses of variance (ANOVAs) for independent and repeated measures. Then, the rate of offline improvement was compared between two age groups using unpaired t-tests (two-tailed). To evaluate the effect of sleep on skill consolidation, multiple regression analyses on the rate of offline improvement as dependent variable and age, sleep durations during night after training (hour), and time intervals from wake-up to perform the retest (hour) as independent variables were conducted, respectively. All analyses were performed in SPSS 19.0. For all analyses, the significance level was $p < 0.05$.

2.3 Results

Performance changes between days and after new learning

Present data indicated that skill performance significantly improved during 24-hours retention intervals without physical practice, confirming that offline improvement took place (Robertson et al., 2004; Walker et al., 2005). We conducted the Group (between factor; 9 *vs* 11 year-old)×Session (within factor; LRN1 *vs* LRN2) ANOVA. In results, there was a significant main effect of Group, indicating that 11 years children exhibited the greater overall performance relative to 9 years children (ANOVA, $F_{1,22} = 5.47$, $p < 0.05$; **Fig. 1A**). Main effect of Session was also significant, confirming that mean performance across the initial three trials at retest was greater than that across the last three trials at training (enhancement; $F_{1,22} = 56.12$, $p < 0.001$). Indeed, planed group-separated ANOVA indicated that 9 and 11 year-old children exerted higher retest performance than at the end of training, respectively (9 year-old, ANOVA, $F_{1,13} = 21.93$, $p < 0.001$; 11 year-old, $F_{1,9} = 40.98$, $p < 0.001$; **Fig. 1B**). There was no significant interaction ($F_{1,22} = 0.86$, $p = 0.36$), and planed group comparisons showed that the rate of offline improvement did not significant differ between two-age groups (unpaired two-tailed t-test, $t_{22} = -0.18$, $p = 0.86$).

The relationship between the rate of gains and sleep durations

Our present data showed that the total sleep duration after skill training was significantly correlated with the rate of offline improvement. Multiple regression analyses were conducted on the rate of offline improvement as dependent variable and age, sleep durations during night after training (hour), and time intervals from wake-up to perform the retest (hour) as independent variables. As a result, sleep duration during night after training had a significant positive effect for the rate of offline improvement (regression analysis, $\beta = 0.60$, $p < .01$; **Fig. 2**), but not age ($\beta = 0.27$, $p = 0.18$) or time intervals since wake-up ($\beta = 0.24$, $p = 0.23$).

Additional subjective ratings: fatigue, concentration, and sleepiness

Additional subjective ratings (that is, sleepiness, concentration, and fatigue) did not significantly differ between two age groups and days, and influenced the rate of offline improvement. We compared subjective rating scores between groups and days using Group (between factor; 9 vs 11 year-old)×Day (within factor; day 1 vs day 2) ANOVA. There were no main effects for all rating scores (ANOVA, $ps \geq 0.52$). However, Group×Day interaction for concentration rating was a marginal significant ($F_{1,22} = 3.41$, $p = 0.08$) but not for sleepiness or fatigue ratings (ANOVA, $ps \geq 0.42$). To evaluate the effects of sleep durations under consideration of difference of concentration, the difference of concentration between days was added into multiple regression analyses as independent variable. Nevertheless, there was certain positive effect of sleep durations on the rate of offline improvement (regression analysis, $\beta = 0.61$, $p < 0.01$).

2.4 Discussions

9 and 11 year-old children showed the significant offline performance improvement across the night after motor training. These results are consistent with previous studies (Dorfberg et al., 2007, 2009), indicating that children have a capability of the skill consolidation without physical training. Although the overall performance was significantly greater in the 11 year-old children than that in the 9 year-old children, the rate of offline improvement did not differ between both age groups. Linear regression analyses shown that the degree of offline improvement was positively correlated with the sleep duration across the night after the training. Taken together, these results suggest that in children sleep is related with a type of skill consolidation.

Most studies have demonstrated that offline skill improvement process depends on sleep (Walker et al., 2002, 2003; Fischer et al., 2002; Nishida & Walker, 2007; Debas et al., 2010; Doyon et al., 2009; Backhaus et al., 2006). Here, we firstly showed that sleep duration after skill training was positively correlated with the degree of offline improvement in children. Present observations consist with previous adult human study (Stickgold et al., 2000). Using the visual discrimination task, Stickgold and his colleagues has shown that the performance improvements between practice sessions was positively correlated with the total sleep durations during the night between practices, suggesting that sleep is necessary for the skill consolidation.

Previous sleep-wake studies in children have shown that declarative memory in children benefit from sleep but skill consolidation does not (Fischer et al., 2007; Prehn-Kristensen et al., 2009; Wilhelm et al., 2008). Present results are inconsistent with these studies, suggesting that sleep is related to the skill consolidation in children. Although we could not absolutely explain this inconsistency, present study differs with previous studies in respect of at least task and age. Fischer et al. (2007) and Prehn-Kristensen et al. (2009) used to the implicit motor learning task. Because the benefit of sleep on the implicit motor training has been controversial (Robertson et al., 2004; Nemeth et al., 2010), this difference might contribute to the discrepancy between our results and previous studies. Alternatively, Age differences might be another contributing factor in this discrepancy. Wilhelm et al. (2009) used to the sequential finger-tapping task, in which was used present study and the benefit of sleep is repeatedly demonstrated. However, their children were the 6 to 8 year-old, whereas children in this study were the 9 to 11 year-old. We speculate that participant's age results in the different results in respect with the effect of sleep in skill consolidation. Previous review literatures have suggested that sleep has an important role only in the hippocampus-dependent memory (Deikelmann et al., 2009, 2010). Also, hippocampus is involved in the explicit motor learning such as a sequential finger-tapping task (Thomas et al., 2004; Schendan et al., 2003). Because hippocampal function seems to be rapidly growing up between 8 and 10 year-old (Townsend et al., 2010), the age of children might be a critical factor contributing to the benefit of sleep in the skill consolidation. Future study should be designed to examine the benefit of sleep on procedural skill consolidation across different age groups.

In present study, sleep duration after motor skill training was observed and recorded by participants' parents and was not directly measured across the sleep periods. A previous adult study based on the subjective report has showed that total sleep duration was significantly correlated with the offline improvements of perceptual skill performance (Stickgold et al., 2000). Therefore, we believe that the sleep duration measurement used in this study could allow us to investigate the correlation between sleep duration and the degree of offline improvements at least to some extent in a reliable way. Recent adult human studies have reported that the rate of offline improvements during sleep is correlated with the specific sleep architectures such as a non-rapid eye movement sleep 2 or sleep spindles rather than with total sleep duration (Walker et al., 2002, 2003; Tucker et al., 2009; Barakat et al., 2011). These evidences encourage the future children studies to elucidate the relationship between the specific sleep architectures during sleep after skill training and the rate of skill enhancement using more direct measurement such as polysomnography.

In summary, present results firstly show that sleep duration after skill leaning is positively correlated with the offline skill consolidation in children. Therefore, sleep seems to be a critical role in skill consolidation in children as well as adults. Given that children train a lot of skill in everyday, understanding the ability of motor skill learning in children might contribute not only their school performance but also to develop the educational and welfare programs.

Study 2

Social rewards enhance the offline improvement in motor skill

4.1 Introduction

Praise is the positive evaluation of another's products, performance, or attributes, where the evaluator presumes the validity of the standards on which the evaluation is based (Kanouse et al., 1981). Praise can boost self-efficacy (Bandura, 1977, 1997) enhance feelings of competence and autonomy (Deci & Ryan, 1983), create positive feelings (Blumendeld et al., 1982), strengthen the association between responses and their positive outcomes (O'Leary & O'Leary, 1977), and provide incentives for task engagement (Madsen et al., 1977). In motor skill learning, for example, praise is hypothesized to provide feedback about the level of participant competence (Catano, 1975), which serves as an incentive to enhance practice efforts (Steers & Porter, 1974). Thus, praise accelerates motor skill performance by enhancing motivation (Catano, 1975; Adam, 1972; Henderlong & Lepper, 2002). This is reasonable because motor skills are initially acquired by repeatedly performing an action during practice. However, learning a motor skill continues to evolve once practice ends (Karni et al., 1995; Brashers-Krug et al., 1996; Muellbacher et al., 2002) through consolidation, which is essential for skill formation and long-term retention (McGaugh, 2000; Walker & Stickgold, 2004; Robertson et al., 2004). There have been no investigations into the effects of praise on skill consolidation. Here, we hypothesize that praise influences the skill consolidation process directly, as opposed to indirectly through motivating further practice.

In the present study we tested this hypothesis through a behavioral experiment designed to manipulate both the timing of the praise given and the participants' expectation of a future test. First, to examine the effects of praise on offline rather than online performance improvements during training, participants were praised only after training was completed. Second, after a 24-h retention interval, all participants performed a ''surprise'' retest of the trained sequence. This minimized the possibility that the participants either physically or mentally practiced the trained sequence prior to the retest. These special considerations allowed us to investigate the direct benefits of praise on skill consolidation.

4.2 Materials and Methods

Participants. Written informed consent was obtained from all participants before participation in the experiment and the study conducted according to the Declaration of Helsinki. If participant was a minor (i.e., 18 or 19 year-old), two different experimenters ensured their ability to make decision and obtained their written informed consent to the participation of this experiment, which were approved by the internal review board of Research Center for Advanced Science and Technology, The University of Tokyo. Fifty-eight healthy volunteers (39 male and 19 females, mean [M] ± standard deviation [SD] = 22.6 ± 4.67 years) participated in this study. None of the participants had a history of neurological, psychiatric, or sleep disorders, and none had had previous training in playing the piano. Based on interviews after the experiments, five participants were excluded from the analyses because they physically or mentally practiced the trained motor sequence after the end of training on day 1. Another five participants were excluded because they noticed or suspected that the evaluation movies that they watched were predetermined. Thus, data from 48 participants (35 males and 13 females; M ± SD = 22.8 ± 5.17 years) were used for analysis (Self group, n = 17; Other group, n = 15; No-praise group, n = 16).

Experimental Procedure. Participants came to the laboratory on two subsequent days. All participants trained on a sequential finger-tapping task (Karni et al., 1995; Debas et al., 2010; Walker et al., 2002, 2003; Fischer et al., 2002; Korman et al., 2007; Manoach et al., 2004) on day 1. The participants were told that evaluators in another room were monitoring their performance through a web camera above the computer monitor, and would comment on their performance after training. However, in reality, their performance was not monitored. After training, all participants received visual feedback about their performance (for example, their learning curve). The participants were then divided into three groups to systematically manipulate the praise that they experienced: 1) participants who watched a movie in which evaluators praised their training performance (Self group); 2) participants who watched the same movie as the Self group, but who were told that it reflected the evaluation of another participant's performance (Other group); and 3) participants who did not watch the movie and who received no praise (No-praise group).

Unbeknownst to the participants, the contents of the movie were predetermined and prerecorded, with actors and actresses portraying the evaluators. At the end of the experiment on day 1, participants were told that they would perform a different task on the next day. On the following day, however, all participants performed a "surprise" retest of the trained sequence; this was intended to minimize the possibility that the participants either physically or mentally practiced the trained sequence prior to the retest, or that those in the Self group, in particular, were more motivated to perform the tasks on day 2. We then examined the effect of the manipulation of praise on the retest performance of the trained sequence.

After the retest, the participants also performed a non-trained sequence, a randomly-ordered tapping task and completed a working memory task. These additional tasks were included to investigate whether the effects of praise were specific to the offline improvement in the trained sequence or induced a more general feeling of happiness that increased motivation to perform well on day 2. If praise enhanced general motivation in the Self group, performance on all additional tasks on day 2 should be better in the Self group than in the Other and No-praise groups.

Sequential Finger Tapping Task. The sequential finger tapping task required participants to press four numeric keys on a standard computer keyboard repeatedly with the fingers of their non-dominant (left) hand as quickly and as accurately as possible for 30-s periods (for details, see Walker et al., 2002, 2003). On day 1, one-half of the participants trained on sequence A ("4-1-3-2-4"), whereas the others trained on sequence B ("2-3-1-4-2"). Training on day 1 consisted of 12 30-s trials with 30-s rest periods between trials, whereas the retest on day 2 consisted of five trials with the same rest interval.

Finger tapping performance was evaluated by the number of correctly tapped sequences per 30-s trial. The offline performance improvement following a night of sleep was defined as the percent increase in mean performance from the last three trials during training on day 1 compared with the first three retest trials on day 2 (Debas et al., 2010; Walker et al., 2002; Fischer et al., 2002; Korman et al., 2007; Manoach et al., 2004).

On day 2, participants also performed the sequence that they had not received training on during day 1 (that is, a participant who trained on sequence A on day 1 performed sequence B on day 2), and the randomly-ordered tapping task, in which stimuli were presented in a random order. Both tasks consisted of five 30-s trials with a 30-s rest period between trials. Performance for the non-trained sequence (NEW) and the randomly-ordered (RAN) tapping was calculated based on the mean number of correctly tapped sequences (NEW) or correctly pressed buttons (RAN) during the five trials.

Manipulation of Praise. After the training on day 1, participants in the Self and Other groups watched a movie in which evaluators praised the training performance. We adopted a movie instead of live praise because predetermined movie can totally control out the variability of evaluators' comments and non-verbal information such as facial expression and intonation. Participants in the Self group were told that the movie represented the evaluation of their own performance during training. The movie consisted of three components: one introduction clip, 12 evaluation clips, and happiness ratings for each clip. In the introduction clip, a man greeted the participant by name to make the evaluation appear more believable and meaningful. Each movie clip was pre-recorded using six actors and six actresses. Ten movie clips contained positive feedback, and two neutral movie clips were included to maintain the attention of participants by making the evaluation less predictable.

In the evaluation movies, praise was directed at the participant's training performance, their attitude during training, or their social ranking relative to other participants (see **Table 1** for examples of evaluators' comments used in this experiment). To rule out the possibility that simply watching the movie might influence the offline improvement in motor skill, we included the Other group, in which participants watched the same movie clips but were told that they represented the evaluation of another participant's training performance. In the introduction clip seen by the Other group, a man used another participant's name. In both the Self and Other groups, regardless of the target of praise, the participants were asked to rate how happy they felt upon watching each movie clip using a seven-point scale (1 = very unhappy, 4 = neutral, and 7 = very happy; the responses for one participant were not collected due to technical difficulties). The order of the evaluation clips was fixed across participants.

After the experiment on day 2, the participants were interviewed to determine whether they had any doubts about the evaluation movies they watched. After this, all participants were fully debriefed.

Working Memory Task. A subset of the participants (n = 35) performed an object working memory task on day 2. A previous study indicated that performance on working memory tasks is highly sensitive to a participant's motivational state (Taylor et al., 2004). In the delayed-matching working memory task, participants were asked to remember three irregular polygons, and were then required to decide while whether a probe stimulus matched any of the three target stimuli (for details, see Taylor et al., 2004). The task was presented in a total of 84 trials.

Alertness, Concentration, and Fatigue During Training and Retest. As it was possible that the subjective state of the participants during training and retest might influence their performance, they completed questionnaires to rate their level of alertness (Stanford Sleepiness Scale rating, Hoddes et al., 1973, translated into Japanese), concentration (1 = not at all, 7 = very concentrated), and fatigue (1 = high level of fatigue, 7 = no fatigue, Hummel et al., 2005) using a seven-point scale at the end of the training and retest periods.

Sleep Duration and Quality the Nights Before and After Training. Because sleep plays an important role in the offline improvement of motor skills (Walker & Stickgold, 2004; Walker et al., 2002, 2003; Fishcer et al., 2002; Debas et al., 2010), sleep duration the night after training was measured by subjective reports and actimetry. Participants were also asked to report the time that they went to bed both the night before and after training, and the time that they woke up on the training and retest mornings. In addition, to confirm the validity of the subjective sleep-duration reports, the physical activity of a subset of participants (n = 26, due to the limited number of available actimetry sensors) was measured from the end of training to the retest time using a standard actimetry sensor. There was a significant correlation between the duration of sleep reported by the participant and that measured by actimetry (Pearson's correlation, $r_{26} = 0.81$, $p < 0.0001$), confirming that the duration of sleep calculated from the subjective reports was reliable. We defined sleep quality as the percentage of true sleep epochs relative to the total sleep intervals automatically determined by AW2 software (Ambulatory Monitoring, Inc., New York).

Statistical Analysis. Statistical analyses were based on a general linear model using analyses of variance (ANOVAs) for independent or repeated measures. Dunnett's test (two-tailed; compared with the Self group) was adopted for multiple-planned comparisons (Dunnett, 1955; Hsu, 1996), based on the hypothesis that the offline improvement in motor skill in the Self group was significantly greater than in the Other and No-praise groups. Analysis of happiness ratings was performed using unpaired t-tests (two-tailed). All analyses were performed using SPSS 19.0 software and the level of significance was $p < 0.05$.

4.3 Results

Performance of the trained sequence. Forty-eight right-handed participants came to the laboratory on two subsequent days (**Fig. 3**). All participants were trained on a sequential finger-tapping task, for which offline improvement (a form of consolidation) has been described elsewhere (Walker & Stickgold, 2004; Robertson et al., 2004; Walker et al., 2002, 2003; Fishcer et al., 2002; Debas et al., 2010). Performance was defined as the number of correctly tapped sequences per 30-s trial. Immediately after training, in order to manipulate praise as an independent variable, participants were divided into three groups (**Fig. 4**): in the "Self group" (n = 17), participants watched a movie in which the evaluators praised their own performance; in the "Other group" (n = 15), participants watched the same movie as the Self group, but were told that it represented the evaluation of another participant's performance; and in the "No-praise group" (n = 16), participants neither watched the movie nor received praise. Participant happiness after watching the clips was subjectively assessed using a seven-point scale (1 = very unhappy, 4 = neutral, 7 = very happy) and the ratings were significantly higher (happier) than 4 (the midpoint) in the Self group (black bar; one-sample t-test, t_{16}

= 12.11, $p < 0.0001$) and the Other group (gray bar; one-sample t-test, $t_{12} = 4.58$, $p < 0.001$). To control out the positive word effect (Hamann & Mao, 2002), we directly compared the happiness rate of both Self and Other groups. We were interested in the effect of the direction of the positive evaluation because when the positive evaluation is directed to "Self", it should be perceived as praise, whereas it should not be when the positive evaluation is directed to "Other". Indeed, participants in the Self group rated the movies as significantly more pleasant than those in the Other group (unpaired t-test, $t_{29} = 2.50$, $p < 0.05$), indicating the successful manipulation of praise in present study.

An analysis of variance (ANOVA) showed that performance at the end of training on day 1 did not significantly differ between the groups ($F_{2,45} = 0.02$, $p = 0.98$; **Fig. 5*A***). In all groups, performance significantly improved between the end of training on day 1 and the retest on day 2 ($F_{1,45} = 267.36$, $p < 0.0001$), confirming the offline improvement on the trained sequence (16, 17, 24–26). The rate of offline improvement differed significantly between the three groups ($F_{2,45} = 3.53$, $p < 0.05$). Improvement was significantly greater in the Self group (19.95 ± 1.85%; **Fig. 5*B***) than in the Other group (14.37 ± 1.33%, Dunnett's test, $p < 0.05$) and the No-praise group (13.14 ±

1.82%, $p < 0.05$), indicating that praise enhanced skill consolidation.

Because several evidences showed that sex of the participants influence the consolidation and recall of different types of memory (Zorawski et al., 2006; Genzei et al., 2012; Felmingham et al., 2012), it is possible that sex of participants interacted with the effect of praise in the offline performance improvements. Therefore, we conducted an additional ANOVA with Group (Self *vs* Other *vs* No-praise) and Sex (Male *vs* Female) as independent variables in the offline improvement. No significant main effect of Sex ($F_{1,42} = .05$, $p = .94$) or interaction between Group and Gender ($F_{2,42} = .62$, $p = .52$) was observed, while the effect of praise was significant ($F_{2,42} = 4.90$, $p < .05$). Although present study was not designed to investigate the effect of sex differences, these results indicate that the effect of praise contributed to the offline improvements in motor skill independently of participants' sex.

In present study, we excluded a total of ten participants from the above-mentioned analyses because they suspected the movie (n = 5) or additionally practiced after the end of practice (n = 5). To evaluate the trend in the performance improvement of these excluded participants, we conducted an additional analysis of offline improvement rates in extra-experimental rehearsal group and suspicion group in comparison with that in the inclusion group (n = 48). According post-hoc test, relative to the average offline improvement rate of included participants (15.94±1.06%), that in extra-experimental rehearsal group was significantly higher (25.66±2.97%, $p < .05$, ANOVA with Dunnett's test) while that in participants who suspected for the movie did not significantly differ (16.96±2.55%, $p = .94$). These data suggest that extra-experimental rehearsal enhance the skill performance through additional exercise, and that suspicion for the movie *per se* did not influence the praise-related enhancement effect in skill consolidation.

Performance on control tasks. An alternative explanation for the Self group's improvement was an increase in general motivation due to praise. To investigate this, the participants were asked to perform a non-trained sequence, a randomly-ordered tapping task, and a working memory task on day 2. There were no significant group differences in performance on either the non-trained sequence (Self, 22.12±0.92; Other, 21.98±1.03; No-praise, 23.27±0.97 sequences per trial; ANOVA: $F_{2,45} = 0.52$, $p = 0.60$,

Table 2) or the randomly-ordered tapping task (Self, 70.16±1.91; Other, 67.89±1.65; No-praise, 69.70±2.76 buttons per trial; $F_{2,45} = 0.30$, $p = 0.74$).

For the working memory task, there were no significant differences between the three groups in either reaction time (Self, 922±47 ms; Other, 912±35 ms; No-praise, 877±25 ms; $F_{2,33} = 0.47$, $p = 0.63$, **Table 3**) or accuracy (the number of correct responses relative to all responses) (Self, 0.71±0.03; Other, 0.80±0.03; No-praise, 0.74±0.03; $F_{2,33} = 1.77$, $p = 0.19$).

Sleep duration and quality during the night after training. Neither sleep duration (measured by subjective reports) nor actimetry measures differed between the groups (Subjective report, $F_{2,45} = 0.02$, $p = 0.98$; Actimetry, $F_{2,45} = 0.52$, $p = 0.60$, **Table 4**). There were also no significant differences between the three groups in sleep quality, as calculated from physical activity during the night after training (Actimetry, $F_{2,45} = 0.49$, $p = 0.62$).

Alertness, concentration, and fatigue during training and retest. Finally, there were no significant differences between the three groups for any of subjective ratings (sleepiness, concentration, and fatigue, ANOVA, p values ≥ 0.06, **Table 4**), indicating that the differences in offline improvement between the groups were not caused by differences in subjective states during training or retest periods.

4.4 Discussions

The purpose of this study was to investigate whether praise following motor training enhances skill consolidation. All groups showed offline skill improvements between the end of training and the retest 24 h later, confirming the results of previous studies (Robertson et al., 2004; Walker et al., 2002; Fischer et al., 2002). Furthermore, our data indicated that praise following motor training enhances consolidation of the learned sequence since the rate of offline improvement was significantly greater in the Self group than in the Other or No-praise groups. As the evaluation video clips viewed by the Self and Other groups were identical except for the instructions indicating to whom the praise was directed, it is unlikely that any physical components in the video clips induced the observed group differences. In addition, other potential factors such as alertness, concentration, fatigue, and quality and duration of sleep did not differ between the groups, so cannot explain the improved consolidation in the Self group.

An alternative explanation of the present result is that praise induces a positive mood or increases the motivation to perform the motor task (Blumenfeld et al., 1982; Catano, 1975; Henderlong & Lepper, 2002), resulting in the greater improvement in performance from day 1 to day 2 performance. If this were the case, however, it would be expected that the uneven performance between the three groups would occur not only for the trained sequence but also on the other tasks. However, the present results showed no significant group differences in these tasks, suggesting that the effects of praise following training were specific to the trained sequence rather than a more general effect on experimental task performance.

Praise is regarded as a reward (Izuma et al., 2008), because praise has two essential components of reward, that is, hedonic and motivational (Schultz, 2000). Praise can induce a feeling of happiness (hedonic component), and also promotes motivation (motivational component, Catano, 1975; Adams, 1972; Henderlong & Lepper, 2002). A recent human neuroimaging study demonstrated that praise activates reward-related areas of the brain, specifically the ventral striatum (Izuma et al., 2008). Rewards are associated with increased dopaminergic activity in the midbrain and striatum, in which dopamine-dependent long-term potentiation (Hosp et al., 2011; Marinelli et al., 2009; Willuhn & Steiner, 2009) has an important role in memory consolidation. The cortico-striatal system plays a critical role in the automatization of the type of motor sequence learning used in the present study (Debas et al., 2010; Doyon et al., 2003; Penhune & Doyon, 2002). Synaptic plasticity represented by long-term potentiation at cortico-striatal synapses strongly depends on the activation of dopamine circuits (Calabresi et al., 2007). As the ventral striatum is the part of the reward system driven by dopamine (Zald et al., 2004), rewards are expected to affect motor skill consolidation. Taken together, present findings suggest that praise functions as "social reward" that induces the dopamine transmission in the striatum, resulting in an enhancement of the motor skill consolidation.

Sleep is another possible contributing factor. There is mounting evidence that sleep is necessary for the offline improvement in the sequential finger-tapping task used in the present investigation (Walker & Stickgold, 2004; Robertson et al., 2004; Debas et al., 2010; Walker et al., 2002, 2003; Fishcer et al., 2002). Although this study was not designed to determine whether sleep is necessary for the praise-related enhancement of skill consolidation, it is reasonable to expect that this enhancement selectively occurs during sleep. Consolidation of a new motor sequence during sleep appears to rely on the covert re-activation of the brain regions that were initially involved in learning the motor skill (Maquet et al., 2000). Recent human neuroimaging studies have shown that several brain areas that were activated during the execution of a memory task are significantly re-activated during sleep (Maquet et al., 2000; Rasch et al., 2007; Diekelmann et al., 2011), and that such re-activation facilitates memory consolidation (Maquet et al., 2000; Rasch et al., 2007). Furthermore, a previous animal study revealed that sleep-dependent re-activation of firing patterns in the ventral striatum took place after reward-related learning (Pennartz et al., 2004). In line with these findings, it is conceivable that the cortico-striatal loop that is modified by praise after the training is then re-activated during sleep, which in turn contributes to the praise-related enhancement of offline, overnight consolidation. This working hypothesis will be the focus of future experimental investigations.

In summary, the present study demonstrated that social rewards directly enhance skill consolidation in humans, and suggests that they have a novel functional effect on the human motor memory system. Further understanding of the effects of social rewards on skill consolidation could help to develop protocols to improve motor skills in educational and rehabilitative contexts.

Conclusion

The goal of current project is to determine the contributing factors enhancing the offline skill consolidation in human motor skill. As mentioned above, I had two hypotheses as following: i) longer sleep durations after skill training benefit the offline skill consolidation in children as well as in adults, ii) praise for own performance enhances the offline performance improvement. To test these hypotheses, I performed two independent behavioral studies. In Study 1, the results showed that in children, post-training sleep durations were positively correlated with the rate of offline improvement, which is a type of skill consolidation, even under controlling out participants' age and time intervals after wake-up. This finding suggests that sleep benefits the offline skill consolidation in children as well as adults. In Study 2, participants who received praise from evaluators exhibited significantly higher offline improvement relative to them in the other groups, while performances in non-trained tasks did not differ across experimental groups. These results suggest that social rewards directly enhance the offline skill consolidation in a certain motor skill. Taken together, sleep and praise might contribute to enhance a form of consolidation in human motor skill.

To date, it is a major challenge to identify the neuronal mechanisms mediating sleep-dependent skill consolidation in human (see for review, Walker, 2005; Diekelmann & Born, 2010). Moreover, it is totally unknown why praise enhance such sleep-dependent skill consolidation. According to previous human and animal evidences, neuronal reactivation, which is that the similar activities that occur during training take place in post-training sleep, seems to be a critical role in sleep-dependent consolidation (Wilson & McNaughton, 1994; Rasch et al., 2007; Antony et al., 2012). Therefore, future investigations should determine whether the praised skill representation is mainly reactivated during subsequent sleep relative to non-praised representations. Simultaneously recording of neuroimaging and electroencephalography during sleep following praise will shed light on this issue.

Although there are enormous evidences investigating some types of motor skills including finger-tapping (Karni et al., 1995; Walker et al., 2002; Fischer et al., 2002) and motor adaptation (Brashers-Krug et al., 1996; Albouy et al., 2012), it is still unclear whether the other important motor skill is consolidated over type. To expand the scope of praise-related enhancement for motor skill consolidation, future studies should examine whether praise facilitate the offline consolidation in another type of motor skill. Specifically, speech production is most important skill because speech necessary for our life. However, there are no explicit evidences demonstrating that human speech is consolidated over time or during sleep, while bird songs were stabilized and sophisticated during sleep (Deregnaucourt et al., 2005; Shank & Margoliash, 2012). Therefore, this issue is an appealing target for the praise-related enhancement.

Finally, present findings showed that sleep benefits human skill consolidation even in children, and that praise is a helpful tool to enhance such sleep-dependent skill consolidation. Although future investigations should determine the scope of such enhancement and explore the underlying mechanisms, these findings might contribute to develop novel approach in educational and rehabilitational contexts.

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Table 1. Examples of the comments from evaluation clips in study 2

Valence of comment	Direction of evaluation	Content
Positive	Performance Social Ranking	Hi, I observed your performance and attitude during the motor task. The tapping became more rhythmical over time. Your performance was great. The number of the pressed buttons in the last trial might be the highest of all the participants I have observed. Thank you.
Positive	Attitude Social Ranking	Hello. I would like to comment on your wonderful performance. First, I think your motor performance on the last trial was the highest of all the participants. In addition, you concentrated very well during the motor task. Thanks for your participation.
Positive	Performance Social Ranking	I can imagine that other evaluators will also give you good feedback. Actually, your performance was amazing and deserves praise. Among the previous participants in the experiment, your performance was the best. Thank you.
Neutral	Performance Social Ranking	Thanks for your participation. The total number of tapped buttons and the speed of tapping increased as practice progressed. Your performance was average relative to the other participants.

Table 2. Performances in the non-learned sequence and random-ordered tapping tasks in study 2

Group	Non-learned sequence task (the number of tapped sequences / 30 s)	Random-ordered tapping task (the number of tapped buttons / 30 s)
Self	22.12 ± 0.92	70.16 ± 1.91
Other	21.98 ± 1.03	67.89 ± 1.65
No-praise	23.27 ± 0.97	69.70 ± 2.76
F	0.52	0.30
P	0.60	0.74

Note. All analyses using independent measure ANOVA.

Table 3. Performance in the working memory task in study 2

Group	Reaction time in High memory-load	Reaction time in Low memory-load	Accuracy in High memory-load	Accuracy in Low memory-load
Self	956 ± 52	899 ± 45	0.72 ± 0.04	0.71 ± 0.03
Other	933 ± 40	892 ± 33	0.78 ± 0.03	0.82 ± 0.03
No-praise	914 ± 28	848 ± 32	0.72 ± 0.03	0.76 ± 0.04
F	0.28	0.61	1.16	2.06
P	0.76	0.55	0.32	0.14

Note. All analyses using independent measure ANOVA.

Table 4. Description for each group in study 2

Measurement	Self group (n = 17)	Other group (n = 15)	No-praise group (n = 16)	Main effect of Group
Descriptions of groups				
Age	22.00 ± 1.03	22.80 ± 1.72	23.50 ± 1.17	$F_{2,45}$ = .34, P = .72
No. of females	6	3	4	
Sleep durations measured by subjective report (hour)				
Before training night	7.38 ± 0.37	7.66 ± 0.48	6.99 ± 1.17	$F_{2,45}$ = .73, P = .49
After training night	7.43 ± 0.55	7.30 ± 0.40	7.31 ± 0.36	$F_{2,45}$ = .02, P = .98
Sleep parameters measured by actimetry (*N* = 26)				
No. of subjects	7	9	10	
Sleep duration (min)	389.8 ± 61.5	448.6 ± 44.3	405.7 ± 21.1	$F_{2,45}$ = .52, P = .60
Sleep quality (%)	95.68 ± 1.35	94.95 ± 0.89	96.22 ± 0.73	$F_{2,45}$ = .49, P = .62
Subjective rating during training				
Alertness (1 - 7)	2.76 ± 0.30	2.73 ± 0.18	2.50 ± 0.20	$F_{2,45}$ = .36, P = .70
Concentration (1 - 7)	5.00 ± 0.26	4.53 ± 0.38	5.63 ± 0.30	$F_{2,45}$ = 3.02, P = .06
Fatigue (1 - 7)	3.32 ± 0.41	3.73 ± 0.37	3.75 ± 0.45	$F_{2,45}$ = .35, P = .71
Subjective rating during retest				
Alertness (1 - 7)	3.12 ± 034	2.67 ± 0.19	2.56 ± 0.20	$F_{2,45}$ = 1.32, P = .28
Concentration (1 - 7)	5.12 ± 0.26	5.00 ± 0.35	5.19 ± 0.32	$F_{2,45}$ = .09, P = .91
Fatigue (1 - 7)	3.65 ± 0.46	3.53 ± 0.45	4.00 ± 0.39	$F_{2,45}$ = .31, P = .74

Note. Mean ± SEM of age, sleep durations (hour), alertness, concentration, and fatigue reported by post-task questionnaires after training and retest. Total time (min) and quality (%) of sleep from the end of training to retest were measured by standard actimetry. The main effect of GROUP estimated by the one-way ANOVAs.

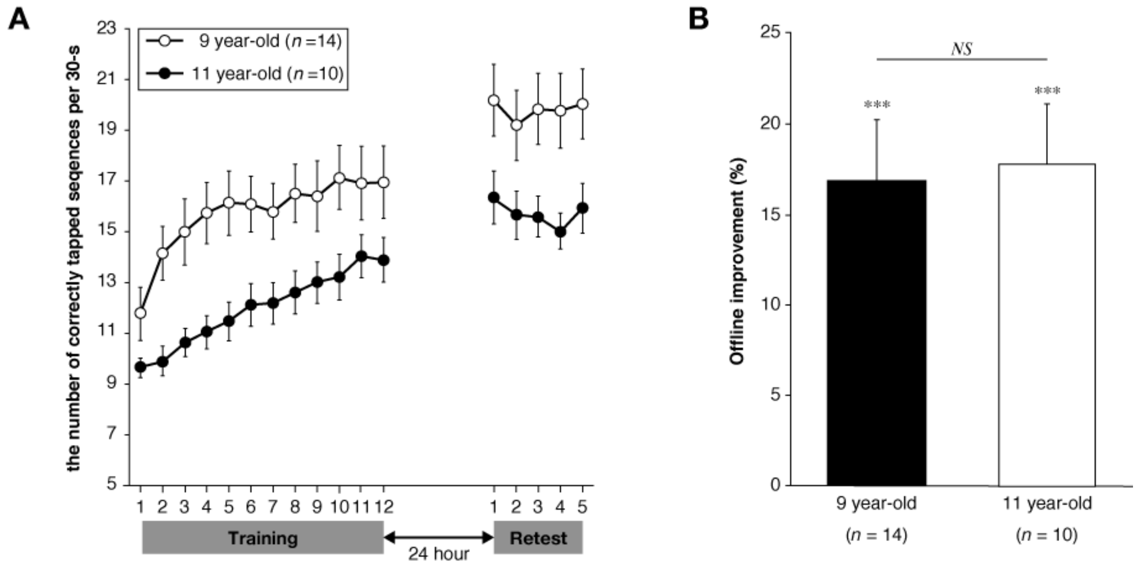

Figure 1. Performances of motor skill and improvements between days in two different age groups. (*A*) Participants in both groups showed the significantly offline improvements, which is the performance improvements from the last three trials at training on day 1 to the first three trials at retest on day 2 (*ps* < 0.001). Black circle represent the mean performance in the 9 year-old group, and that in 11 year-old group plotted as open circle. (*B*) Totally, the skill performance in the 11 year-old children was significantly greater than that in the 9 year-old children ($p < 0.05$). However, the rate of offline improvements did not differ between both age groups (two-tailed unpaired t-test; $p = 0.51$). Black or white bar represents the 9 or 11 year-old group. Error bars indicate the standard error of the mean (SEM). ***$p < .001$; **$p < .01$ (repeated-measure ANOVA).

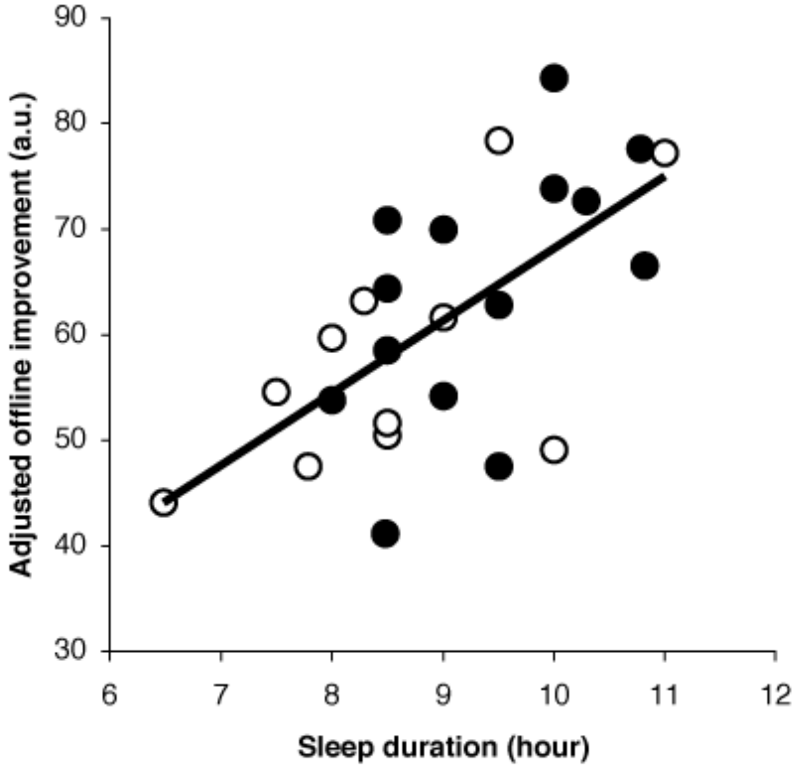

Figure 2. Sleep quantity and performance improvements in Study 1. The rate of offline improvements, which is the performance improvements between days, was significantly correlated with the sleep duration across the night after motor training (regression analysis; $\beta = 0.65$, $p < 0.05$). Vertical axis represents the adjusted improvements ruling out the effect of age and the waking durations on day 2 estimated from the results of the regression analysis. Horizontal axis indicates the sleep duration (hour) during the night after motor training. Black or white points represent the individual data in the 9 or 11 year-old children, respectively. Solid line is linear regression fit.

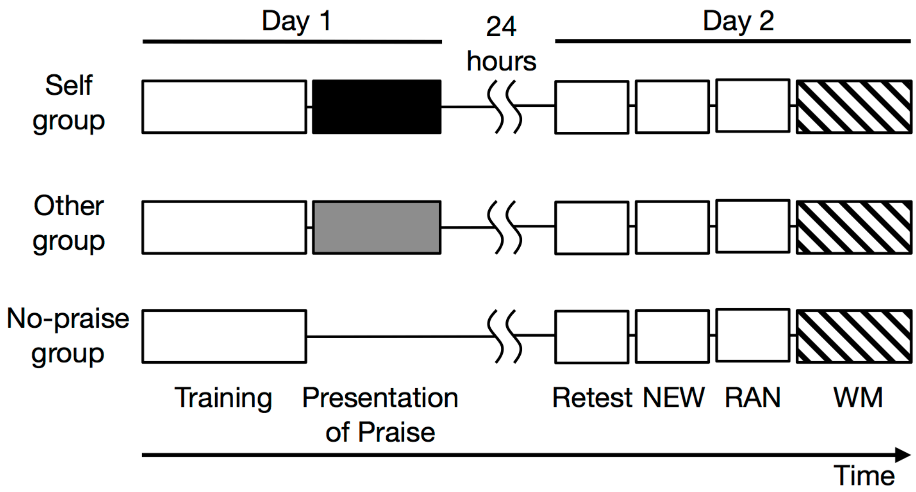

Figure 3. Experimental design in Study 2. All participants were initially trained on a sequential finger-tapping task. They were then divided into three groups according to whether they received praise for their own training performance (Self group), praise for another participant's training performance (Other group), or no praise (No-praise group). The next day, participants completed a surprise retest of the trained sequence, a non-trained sequence (NEW), randomly-ordered tapping (RAN), and a working memory (WM) task.

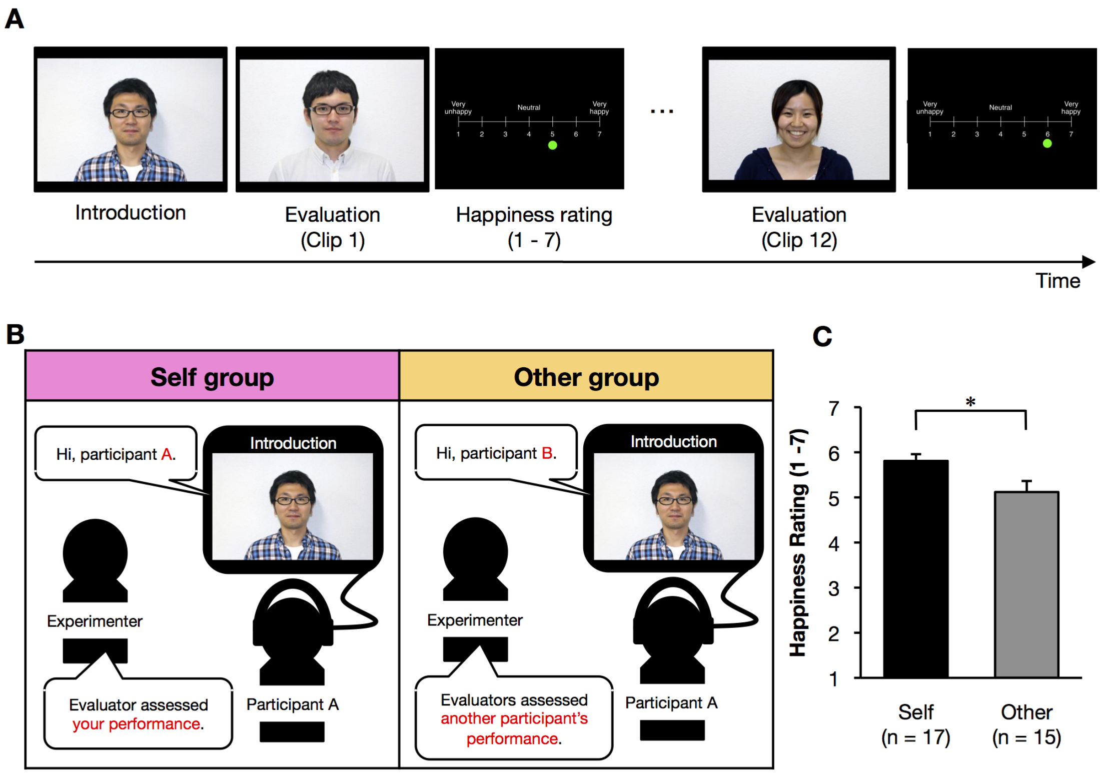

Figure 4. Manipulation of praise. (*A*) The sequence of events in the movie. The introduction clip was followed by 12 evaluation clips in a fixed order. After each evaluation clip, the participant was asked to rate their subjective happiness using a seven-point scale. (*B*) The instructions and the introduction clip differed between the Self and Other groups. In the Self group, participants were told that the movies represented an evaluation of their own training performance. Participants in the Other group were told that the movies represented the evaluation of another participant's performance. (*C*) The subjective judgment of participant happiness using a seven-point scale (1 = very unhappy, 4 = neutral, 7 = very happy). Error bars indicate the standard error of the mean (SEM). *$p < 0.05$ (unpaired two-tailed t-test). The subject of the photograph has given written informed consent, as outlined in the PLoS consent form, to publication of their photograph.

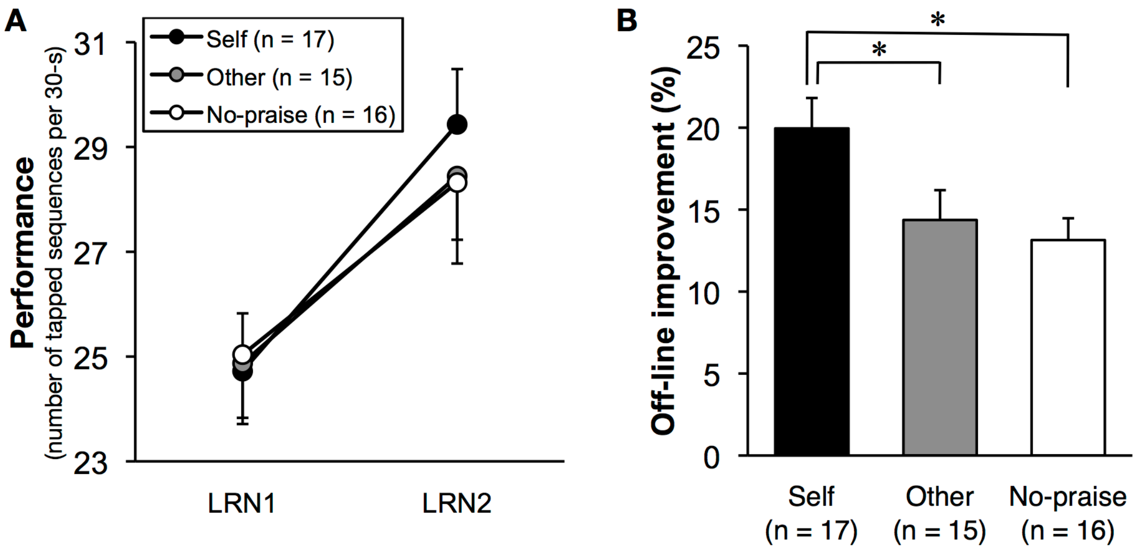

Figure 5. Results in Study 2. (*A*) Mean performance during the last three training trials on day 1 (LRN1) and the first three retest trials on day 2 (LRN 2). All groups showed offline improvements on the trained sequence. (*B*) The rate of offline improvement, the percent increase from LRN1 to LRN2, was significantly greater in the Self group than the Other and No-praise groups. Black, gray, and white points or bars represent the Self, Other, and No-praise groups, respectively. Error bars indicate the standard error of the mean (SEM). $*p < 0.05$ (Dunnett's test).