

EXOSKELETONS

Surmounting the ceiling effect of motor expertise by novel sensory experience with a hand exoskeleton

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For trained individuals such as athletes and musicians, learning often plateaus after extensive training, known as the “ceiling effect.” One bottleneck to overcome it is having no prior physical experience with the skill to be learned. Here, we challenge this issue by exposing expert pianists to fast and complex finger movements that cannot be performed voluntarily, using a hand exoskeleton robot that can move individual fingers quickly and independently. Although the skill of moving the fingers quickly plateaued through weeks of piano practice, passive exposure to otherwise impossible complex finger movements generated by the exoskeleton robot at a speed faster than the pianists’ fastest one enabled them to play faster. Neither a training for fast but simple finger movements nor one for slow but complex movements with the exoskeleton enhanced the overtrained motor skill. The exoskeleton training with one hand also improved the motor skill of the untrained contralateral hand, demonstrating the intermanual transfer effect. The training altered patterns of coordinated activities across multiple finger muscles during piano playing but not in general motor and somatosensory functions or in anatomical characteristics of the hand (range of motion). Patterns of the multifinger movements evoked by transcranial magnetic stimulation over the left motor cortex were also changed through passive exposure to fast and complex finger movements, which accompanied increased involvement of constituent movement elements characterizing the individuated finger movements. The results demonstrate evidence that somatosensory exposure to an unexperienced motor skill allows surmounting of the ceiling effect in a task-specific but effector-independent manner.

INTRODUCTION

Mastery of the outstanding skills characterizing experts accompanies extensive practicing. However, practice does not always guarantee improvement. Recently, an increasing number of studies have demonstrated that the amount of training accounts for less than half of mastery of expertise, which questions the impacts of deliberate practice (1–4). This is particularly important for trained individuals who seek to develop further sophisticated skills but face a challenge in achieving it because of a diminished learning gain after extensive training for stabilizing the skill, the so-called ceiling effect (5). To surmount limits of expertise, it is essential to establish unique ways of training that do not rely only on the amount of training or early training in childhood (6–8). Recent studies have reported the effectiveness of specialized sensorimotor training for well-trained individuals (9, 10). However, most of these studies have focused on simple motor tasks (e.g., repetitive motions with a single finger). It remains elusive what training strategies enhance the complex motor skills of trained individuals, which limits both a comprehensive understanding of the neuroplastic mechanisms of the sensorimotor system and the development of training methods that enable the enhancement of overtrained skills.

A common dilemma in further sophisticating complex motor skills that have undergone extensive training is the absence of prior physical experience with the extraordinary skill to be acquired. This can make it challenging for learners to obtain precise error information between the desired and produced body movements because of imprecision of motor simulation and/or motor imagery of the unexperienced complex skill (11–14). Thus, movement reorganization for further sophisticating trained motor skills can be achieved exploratorily for minimizing

performance errors and/or maximizing reward (15, 16). One potential method to optimize this learning is to provide sensory information on the target motor skill (17), such as vision-based observation learning (18, 19) and somatosensory learning through exposure to passively generated movements (20, 21). For example, limb motions passively generated by a robot facilitated accuracy of the limb movements and postural control in healthy individuals and patients with movement disorders (20–23). One may therefore postulate that exposure to sensory stimuli representing complex motor skills such as dexterous finger maneuvers similarly further improves overtrained skills. However, most previous studies that addressed the effects of passive sensory experience on motor skills have investigated simple tasks, which include reaching, grasping, walking, and standing (24–26). Several studies also reported learning of complex motor skills such as Braille reading, typing, and piano playing through haptic devices by nonexperts (27–29). Whether exposure to previously unexperienced sensory experiences of a complex motor skill can further improve the well-trained skill and thereby overcome the ceiling effect has not been addressed.

To test this, we used a custom-made exoskeleton robot for the hand that can move the individual fingers independently for both flexion and extension. Passive training effects with the robot were predicted on the basis of the observation that tuning movement patterns of overlearned skills such as standing and running by attaching an exoskeleton robot to the limb enhanced motor performance (30–34); however, it remains unknown whether the enhancing effect is limited only when the robot is attached to the limb. To identify what sensory experience can enhance a complex overtrained motor skill, the exoskeleton robot was used by expert pianists to experience different patterns of multifinger movements at different speeds. We postulated that somatosensory inputs of unexperienced motions, which involved faster and more accurate performance of complex multifinger movements than voluntarily produced motion, specifically enhance the motor skill of trained pianists, even after the skill

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plateaus through extensive training. By evaluating patterns of multifinger movements evoked by the noninvasive brain stimulation, we further tested whether neuroplastic adaptation of the corticospinal system underlies enhancement of the overtrained motor skill through passive training.

RESULTS

Three studies were performed to test whether passive somatosensory training using a hand exoskeleton robot enhanced highly skilled finger movements in trained individuals. In total, 118 pianists participated in the studies.

Study 1: Overcoming limits of overlearned motor skills through passive training

We first tested whether exposure to passively controlled finger movements enhanced the performance of skillful finger movements after the skill plateaued through long-term active practicing of the motor skill. Thirty pianists participated in the experiment, which consisted of pretraining, pretest, intervention, posttest, and retention test. In the intervention session, the pianists were exposed to passive finger movements generated by a hand exoskeleton robot that could move the individual fingers independently (Fig. 1A and movie S1).

To evaluate motor skill during the pretraining session at home, we developed a custom-made sensor system that can be placed on piano keys and record the vertical key position. The system was then given to 30 pianists who practiced the designated motor task with the piano (Fig. 1B) at home every day over a period of 2 weeks. On the 1st, 5th, 10th, and 14th days of the daily practice, they also performed the task as quickly and accurately as possible to assess the practice effect. After this pretraining, pianists were asked to participate in an experiment that involved passive training with the hand exoskeleton robot at the laboratory for 30 min. Thirty participants who underwent the home training were randomly assigned to two groups according to whether the pattern of the fast finger movements generated by the exoskeleton robot was complex or simple (“complex group” and “simple group,” respectively) (Fig. 1C inset; see Materials and Methods for more details). For both groups, each finger was moved at a rate of 4 Hz (four repetitions of flexion-extension movements per second) by the exoskeleton, which was faster than the maximum rate of voluntary piano keystrokes in these tasks (on average, 2.3 strikes per second for the present pianists). Before and after the intervention, each participant actively performed the motor task with the piano as quickly and accurately as possible, which involved successive piano keystrokes with the complex finger movement used in the pretraining session (movies S2 and S3). One day after the intervention in the laboratory, the skill was assessed at home again to evaluate the retention effect of the intervention.

Figure 1C illustrates the time course of the motor skill before and after the passive training, displaying the group mean of the interkey-stroke interval (IKI) when performing the designated task on the piano as quickly and accurately as possible. During the pretraining practice period at home, there was no statistically significant change in the IKI through the practice in either group, which confirmed the ceiling effect of the target motor skill. The IKI became shorter after the passive training, specifically in the group that underwent passive training with the complex movement pattern (complex group)

(pretest: 434.6 ± 10.6 ms, posttest: 407.4 ± 7.7 ms; mean \pm SEM across participants) but not in the group that underwent passive training with the simple movement pattern (simple group) (pretest: 437.8 ± 10.3 ms, posttest: 436.1 ± 10.2 ms; mean \pm SEM across participants) (see also fig. S1A). The decrease in the IKI was maintained 30 min after the intervention. One day after the intervention, the motor performance exhibited no statistically significant difference from that immediately after the training. A two-way mixed-design analysis of variance (ANOVA) statistics test confirmed both an interaction effect between group and session and a main effect of session (table S1), and post hoc tests with correction for multiple comparisons identified statistically significant differences between the pretest and each of the two posttest sessions specifically after the training with complex finger motions (complex group) as well as groupwise differences for the two posttest sessions (in the dotted box in Fig. 1C). These results confirmed that the passive training with the complex pattern of movements specifically improved skillful finger movements in piano playing, although the skill plateaued after conventional repetitive practice. Figure S1B further illustrates the differential value of the IKI between the pretest and posttest sessions for each of four fingers in the two groups who underwent different types of training (complex group and simple group). Although the decrease was larger in the complex group than in the simple group, the difference was not present between the fingers. A linear mixed model using the group (the complex and simple groups) and finger as fixed effects yielded neither an interaction effect between group and finger nor a main effect of finger (table S2), which indicated a uniform effect of passive training with the complex movements across fingers.

To evaluate the effect of the passive training on the timing precision of finger movements in keystrokes, the intratrial average and variability of the timing error between two simultaneous strikes across successive strikes were compared among the pretest, posttest, and retention sessions in both groups (fig. S2, A and B). The intratrial averages at the pretest, posttest, and retention were 3.1 ± 2.6 , 2.2 ± 4.3 , and -1.1 ± 3.5 ms, respectively, for the group undergoing the training with the complex motion. The averages were 3.3 ± 3.0 , 2.9 ± 3.7 , and 2.7 ± 3.3 ms for the pretest, posttest, and retention, respectively, in the group undergoing the training with the simple motion (mean \pm SEM across participants). A two-way mixed-design ANOVA statistics test yielded neither an interaction effect between group and session nor a group effect for both the interstrike average and variability of timing error between two simultaneous strikes (table S3). The results rejected the possibility that faster performance of repetitive keystrokes after the training was due to the speed-accuracy trade-off.

Changes in muscular coordination through passive training

To further address effects of the passive exoskeleton training on neuromuscular control of multifinger movements, patterns of activities of the intrinsic and extrinsic finger muscles were compared between the pretest and posttest for the complex and simple groups in study 1. The patterns of the activities were extracted by the nonnegative matrix factorization (NMF) algorithm (15, 35, 36). On the basis of the root mean square activities of the muscles during the period of one IKI (Fig. 2, A and B), two patterns of coordinated muscular activities were extracted, which consisted of the time-varying waveforms representing muscular activities (Fig. 2C) and the weighting coefficients of the individual muscles (Fig. 2D). According to the muscles active in each pattern and the timing of

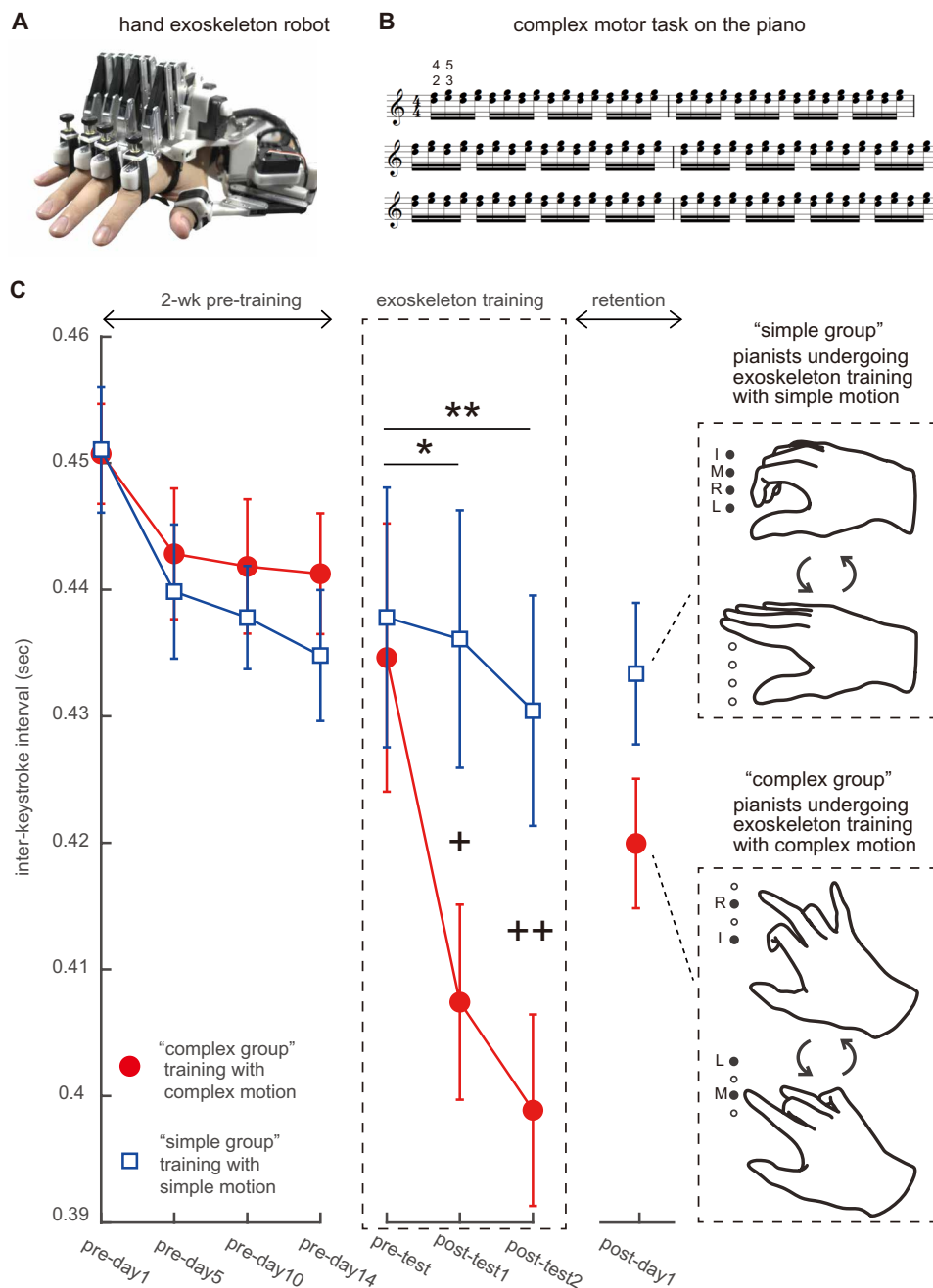


Fig. 1. Results of the assessment of motor skills before and after the passive finger training (study 1). (A) Hand exoskeleton robot attached to the digits of the right hand. The device can flex and extend the MP joints of the individual digits. (B) A piano task with a complex movement pattern. The task was characterized by alternate repetition of simultaneous strikes of every other key (D and F keys) with the right index and ring fingers and simultaneous strikes of their adjacent keys (E and G keys) with the right middle and little fingers. This chord-trill task involved repetition of two sets of simultaneous strikes of the two keys while leaving one white key in between (major third interval), using the right index and ring fingers for one set and the right middle and little fingers for another set, at a predetermined loudness (mezzo forte). (C) A time course of motor performance during active piano practice at home and before and after passive exoskeleton training. The home-based pretraining session included 2 weeks of daily piano practice at home. On the 1st, 5th, 10th, and 14th days of the pretraining, the performance of the keystroke task at the fastest tempo was assessed. Subsequently, in the laboratory, the performance of the keystroke task was assessed before, immediately after, and 30 min after the passive somatosensory training with either complex or simple movement patterns (pretest, posttest1, posttest2). * and + indicate a statistically significant session-wise and groupwise difference, respectively. * and +: $P < 0.05$, ** and ++: $P < 0.01$. One day after the exoskeleton training at the laboratory, the retention effect was assessed at home with the same assessment approach as in the pretraining session. The red filled circle and blue open square plots indicate the passive somatosensory training with complex motion and simple motion patterns, respectively. Inset: Two training tasks involved passive finger motions generated by the exoskeleton robot. The complex task involved a succession of simultaneous flexion of the index and ring fingers with simultaneous extension of the middle and little fingers and vice versa (right bottom). The simple task involved repeating simultaneous flexion and extension of the index, middle, ring, and little fingers. These two tasks therefore represent the individuated and synergistic movements between the fingers. In total, 30 pianists participated in the study. Pianists who underwent a simple and complex task during the training are referred to as the simple and complex groups, respectively.

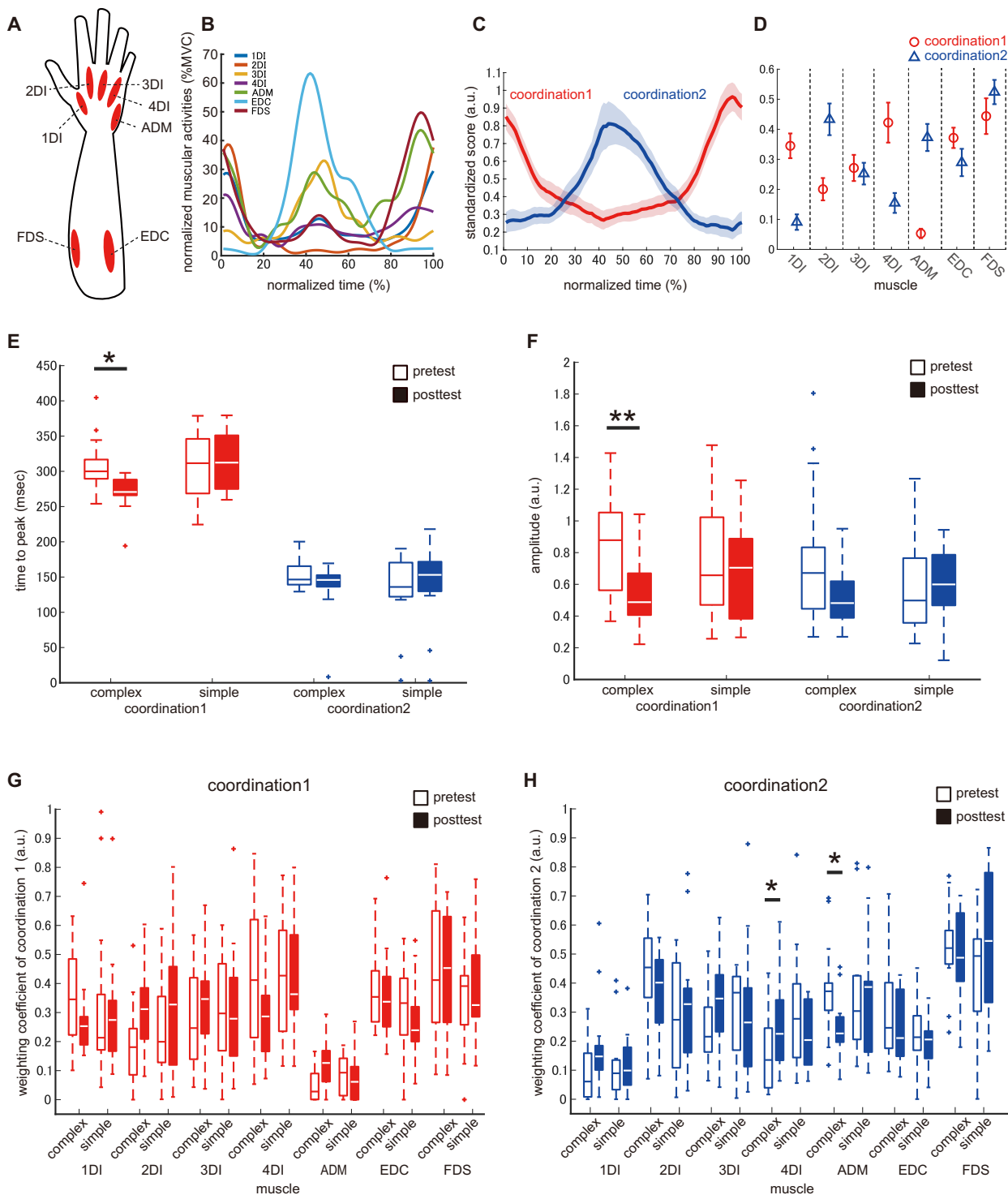


Fig. 2. Results of the assessment of muscular activities before and after the passive finger training (study 1). (A) Schematic drawing of the seven intrinsic and extrinsic finger muscles recorded in the experiment. (B) The original activity patterns of the individual measured muscles during one IKI in the complex task. Both times 0 and 100 represent the moments of simultaneous keystrokes with the index and ring fingers. The vertical axis indicates the normalized muscular activities based on the MVC. (C and D) A representative result of the NMF analysis based on the muscular activities of one participant, which were decomposed into two distinct time-varying patterns of muscular activities [coordination 1 and 2 in (C)] and the weighting coefficients of the individual muscles of the two coordination patterns (D). The plots in red and blue represent coordination 1 and 2, respectively. The shaded area (C) and error bar (D) represent one SE. (E) Group means of the time to the peak muscular activities (in milliseconds) for coordination 1 (red) and coordination 2 (blue) for the participants who underwent passive training with complex motions (left) and simple motions (right) in the pretest (open bar) and posttest (filled bar) sessions. * $P < 0.05$ statistically significant difference between groups. (F) Group means of the amplitude of the peak muscular activities for coordination 1 (red) and coordination 2 (blue). ** $P < 0.01$ statistically significant difference. (G and H) Group means of the weighting coefficients of seven measured muscles for coordination 1 [red in (G)] and coordination 2 [blue in (H)]. * $P < 0.05$ statistically significant difference. a.u., arbitrary units.

the peak activity, the two patterns represented muscular activities related to the simultaneous keystrokes by the index and ring fingers (coordination 1) and those related to the simultaneous keystrokes by the middle and little fingers (coordination 2). Therefore, the two coordination patterns characterized muscular activities responsible for two distinct events in the repetitive keystrokes. On the basis of the waveform of the muscular activities, the time to and the magnitude of the peak activities (Fig. 2, E and F) were computed for each coordination. Both the time to the peak activity and the peak magnitude were lower at the posttest than at the pretest, specifically for coordination 1 in the group that underwent training with the complex movements (Fig. 2, E and F). A two-way mixed design ANOVA statistics test confirmed an interaction effect of group and session for both the time to the peak activity and the peak magnitude of coordination 1 but not for coordination 2 (table S4). The interaction effect indicated a session-wise difference only in the complex group. Figure 2 (G and H) represents the group means of the weighting coefficients of the individual muscles for coordination 1 and 2, respectively. Although the session-wise difference was not evident for any muscles in coordination 1 in either group (Fig. 2G), there were session-wise differences at the fourth dorsal interossei (4DI) and abductor digiti minimi (ADM) muscles in coordination 2 only in the complex group (Fig. 2H). Three-way mixed-design ANOVA statistics tests confirmed an interaction effect of group, session, and muscle for coordination 2 but not for coordination 1 (table S4). The interaction effect indicated that the groupwise difference in the change in the weighting coefficient through the training varied across muscles. These results indicated that passive exoskeleton training with the complex movement pattern brought about nonuniform changes in the spatio-temporal pattern of multifinger muscular coordination.

Effects of passive training on sensorimotor functions and anatomical features of the fingers

To test whether the passive training changed general sensorimotor functions and anatomical features of the fingers, the strength, movement independence across fingers, agility, and anatomical range of motion of each finger were compared between the pretest and posttest sessions in the complex and simple groups. Table S5 summarizes the results. For each of these features, a linear mixed model was developed using the group and session as the fixed effects and the finger and participant as the random effects. The results yielded no interaction effect between group and session for all features. Similarly, to test whether the passive training altered somatosensory functions, a psychophysics experiment was performed to assess perception in discriminating the movement duration of the passively generated motions between the two fingers (table S6). Two fingers were passively moved, and the motion was controlled with different movement durations within the predetermined range of motion (i.e., equivalent to perception of movement velocity). The discrimination threshold did not differ between the sessions in either group, which was confirmed by mixed-design ANOVA statistics tests showing neither interaction nor main effects of group and session. These results indicated that the present passive training did not enhance sensorimotor functions that were not specific to piano playing and anatomical adaptation of the fingers.

Study 2: Specific effects of the passive training on dexterous motor skills

To identify the movement features responsible for enhancement of skilled finger movements through the passive exoskeleton training

and to explore the underlying mechanisms, study 2 compared the effects of a variety of training methods. Figure 3 illustrates the group means of the IKI averaged across strikes while performing the complex and simple motor tasks on the piano with the trained right hand and the untrained left hand before and after five different sets of interventions. In total, 60 pianists participated in the experiment, and they were assigned randomly to one of five groups. In two groups, the participants underwent passive exoskeleton training with complex and simple patterns of multiple finger movements at a movement rate of 4 Hz (i.e., four repetitions of flexion-extension per second at each finger), which was faster than the movement rate when the pianists actively performed the complex task on the piano in the pretest (average keystroke rate = 2.3 Hz, IKI = 433.5 ± 40.5 ms) (“complex-fast” and “simple-fast” groups, respectively). In another group, the participants underwent passive training with a complex movement pattern slowly at a movement rate of 1 Hz (“complex-slow” group). In the active control group, the participants played the piano with the complex finger movement pattern at a rate of two keystrokes per second (“active” group). They took a rest for 10 s every minute of the performance. In the passive control group, the participants took rest (“rest” group). After the intervention, the average IKI during repetitive piano keystrokes involving the complex finger movements with the right hand decreased only in the complex-fast group but not in the remaining four groups (Fig. 3A). This improvement was also evident for the untrained left hand, which confirmed the intermanual transfer effect of the training (Fig. 3B). Two-way mixed-design ANOVA tests confirmed both an interaction effect between group and session and a main effect of session for both hands (table S7), yielding different training effects across the groups. For the repetitive keystrokes involving the simple movement pattern, the average IKI of the right hand was not different between the sessions in any group (Fig. 3C). A two-way mixed-design ANOVA showed neither an interaction nor a main effect in this simple task. These results demonstrated the specific effects of the passive somatosensory training with complex-fast multifinger movements on the trained motor skill for both the trained and untrained hands.

Study 3: Hand kinematics encoded in the corticospinal system

This study tested whether passive exposure to multifinger movements brought about neuroplastic changes in the corticospinal system. Twenty-eight pianists participated in the neurophysiological experiment that consisted of the pretest, intervention, and posttest sessions. The intervention session was the same as the one in study 1; the participants were divided into two groups undergoing the exoskeleton training with either the complex or simple multifinger movements (the complex and simple groups) with the right hand at a rate of 4 Hz for 30 min. Each of the pretest and posttest sessions consisted of the behavioral and neurophysiological assessments. The behavioral assessment was performed in the same manner as study 1, namely, the fastest piano keystrokes with the complex pattern of multifinger movements with each hand for 5 s. The keystroke task was repeated over five trials. The results replicated the result of study 1 by confirming an interaction effect between group and session on the IKI on the basis of the mixed-design two-way ANOVA statistics test for both the right hand [$F(1, 26) = 31.25, P < 0.01, \eta^2 = 0.092$] and the left hand [$F(1, 26) = 35.97, P < 0.01, \eta^2 = 0.103$]. For the right hand, the group means of the IKI at the pretest and posttest

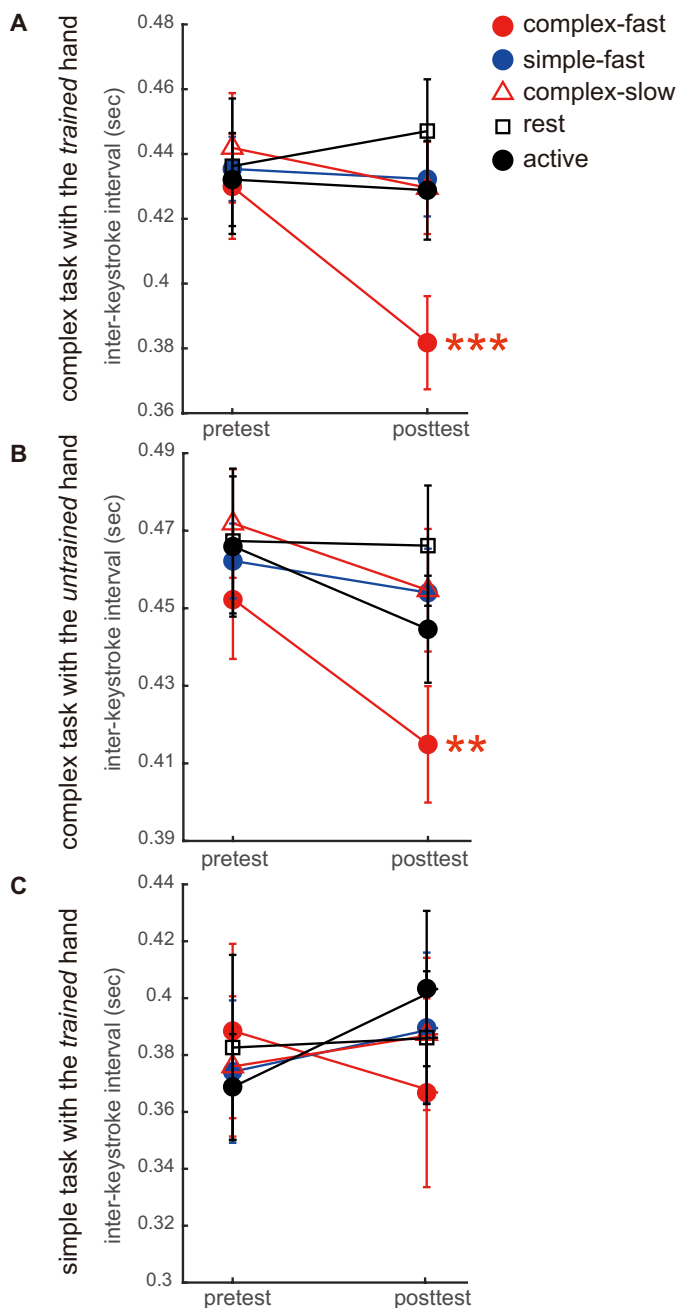


Fig. 3. Results of the motor performance assessment before and after each of the five different sets of interventions (study 2). The horizontal axis represents the pretest and posttest sessions, whereas the vertical axis represents the IKI at the fastest tempo while performing the complex task on the piano with the trained hand (A), when performing the complex task on the piano with the untrained hand (B), and when performing the simple task on the piano with the trained hand (C). The symbols represent the participants in the groups who underwent different interventions: passive training with fast complex motions (filled red circle, complex-fast group), passive training with fast simple motions (filled blue circle, simple-fast group), passive training with slow complex motions (open red triangle, complex-slow group), rest (open black square, rest group), and active piano practice (filled black circle, active group). ** $P < 0.01$ and *** $P < 0.001$. In total, 60 pianists participated in the study.

were 439.6 ± 56.4 and 386.3 ± 44.8 ms, respectively, for the complex group and 433.5 ± 50.1 and 447.0 ± 64.4 ms, respectively, for the simple group. For the left hand, the group means of the IKI at the pretest and posttest were 490.7 ± 72.9 and 438.3 ± 54.1 ms, respectively, for the complex group and 485.1 ± 67.6 and 499.0 ± 68.8 ms, respectively, for the simple group. Post hoc testing confirmed the session-wise difference only for the complex group ($P < 0.01$ for both the right and left hands). For the session-wise difference in the IKI, there was a statistically significant but weak correlation between the trained and untrained hands [correlation coefficient (r) = 0.57, $P = 0.03$]. Using the result of the posttest session, we first tested whether the training effect was evident immediately after the intervention and, second, whether the performance was improved by undergoing the posttest session. To test the first hypothesis, the IKI of the initial four keystrokes at the first trial of the posttest was compared with one of the last four keystrokes of that trial. A two-way mixed-design ANOVA demonstrated that neither an effect of strike [$F(1, 26) = 2.13$, $P = 0.156$, $\eta^2 = 0.001$] nor an interaction effect of strike and group [$F(1, 26) = 1.85$, $P = 0.186$, $\eta^2 = 0.001$] was statistically significant, confirming no within-trial difference. To test the second hypothesis, the IKI was compared across the trials of the posttest session. Neither an interaction effect of group and trial [$F(1, 26) = 0.16$, $P = 0.690$, $\eta^2 = 0.0004$] nor a trial effect [$F(1, 26) = 0.196$, $P = 0.662$, $\eta^2 = 0.0004$] was statistically significant, confirming no between-trial difference at the posttest. These two results did not support that the enhanced motor performance after the passive training resulted from motor learning through repetitive keystrokes during the posttest session.

The neurophysiological assessment was performed using transcranial magnetic stimulation (TMS) at the pretest and posttest sessions. The stimulation was applied over the primary motor cortices of each of the right and left hemispheres [around the hotspot of the flexor digitorum superficialis (FDS)] (Fig. 4A), and the evoked finger movements were recorded with the data glove (Fig. 4B; see Materials and Methods in detail) (37). Patterns of the multifinger movements evoked by the stimulation were analyzed by tensor decomposition (38), and the movement features that characterized the extracted spatial and temporal modules were compared between the pretest and posttest in both groups for each hand. In total, a weighted linear combination of the five sets of temporal, spatial, and trial modules accounted for 74.1 and 77.2% of the total variance for the right and left hand, respectively. Figure 4C illustrates the results of tensor decomposition for the right hand. Temporal modules of the five tensors that represent muscular activation patterns were commonly characterized by movement initiation around 100 ms after the stimulation, which reached its peak around 200 ms after the stimulation. The spatial modules of the five tensors described different patterns of the movement covariation between the joints. The first and second spatial modules (i.e., tensors 1 and 2) characterized simultaneous motions of the metacarpophalangeal (MP) and proximal-interphalangeal (PIP) joints in the same direction, respectively, which were similar to the grasping motion. By contrast, the remaining three spatial modules (i.e., tensors 3, 4, and 5) were characterized by individuated movements between the fingers. The third module (tensor 3) primarily involved the PIP joint rotation of the index finger, whereas the fourth module (tensor 4) described its opposite rotation at the PIP joint of the middle finger. The fifth module (tensor 5) was characterized mainly by the motions of the MP joints

[$F(1, 26) = 7.56, P = 0.01$] and between session and component [$F(1, 110) = 4.30, P = 0.04$]. These interaction effects indicated that the session-wise difference differed between the groups and between the tensors. Post hoc tests indicated session-wise differences in the complex group for tensors 4 and 5 and in the simple group for tensor 1. Unlike the right hand, there was no statistically significant session-wise difference in the patterns of the evoked movements of the left hand (Fig. 5). A linear mixed model yielded no interaction effect among group, session, and tensor [$F(1, 110) = 0.20, P = 0.66$], between session and group [$F(1, 26) = 0.60, P = 0.45$], or between session and tensor [$F(1, 110) = 2.59, P = 0.11$]. These findings indicated that patterns of multifinger movements evoked by the noninvasive stimulation on the motor cortex changed specifically through the passive training with complex finger movements, which was evident only in the trained right hand.

DISCUSSION

The present study tested whether exposure to passive somatosensory experiences of fast and complex finger movements generated by a hand exoskeleton robot enhanced the performance of overlearned skills in expert pianists. Even when the skill plateaued after weeks of piano practice, passive training of the fast and complex motor skill with the robot further facilitated the maximum rate of repetitive piano keystrokes involving fast and complex multifinger

movements. This training effect was also evident in the contralateral untrained hand, supporting the intermanual transfer effect. These findings indicate that passive performance of fast movements requiring complex multifinger coordination enhances the maximum speed of performing the trained movement sequence for both the trained and untrained hands of the pianists. This result highlights the importance of the hand exoskeleton allowing skilled individuals to achieve otherwise impossible motions. In contrast, when the fingers underwent a simple pattern of movements similar to grasping, experiencing motions faster than the voluntary motions did not yield any change in the fastest finger movements. Similarly, no training effect was observed when the fingers were moved with the complex multifinger coordination pattern at speeds much slower than the fastest movement. These two null effects further suggest that exposure to somatosensory experience of a dexterous motor skill that has not been previously experienced is effective as a way of surmounting the ceiling effect of the overtrained motor skill. The results thus highlight the importance of making the best use of augmentation technology for enhancing experts' expertise.

A question is what neuroplastic adaptation underlies the facilitatory effect of passive training. Neither motor functions nor anatomical characteristics of the hand changed after the training. The somatosensory perception of movement speed was also not changed, which suggests independence of this somatosensory function of the

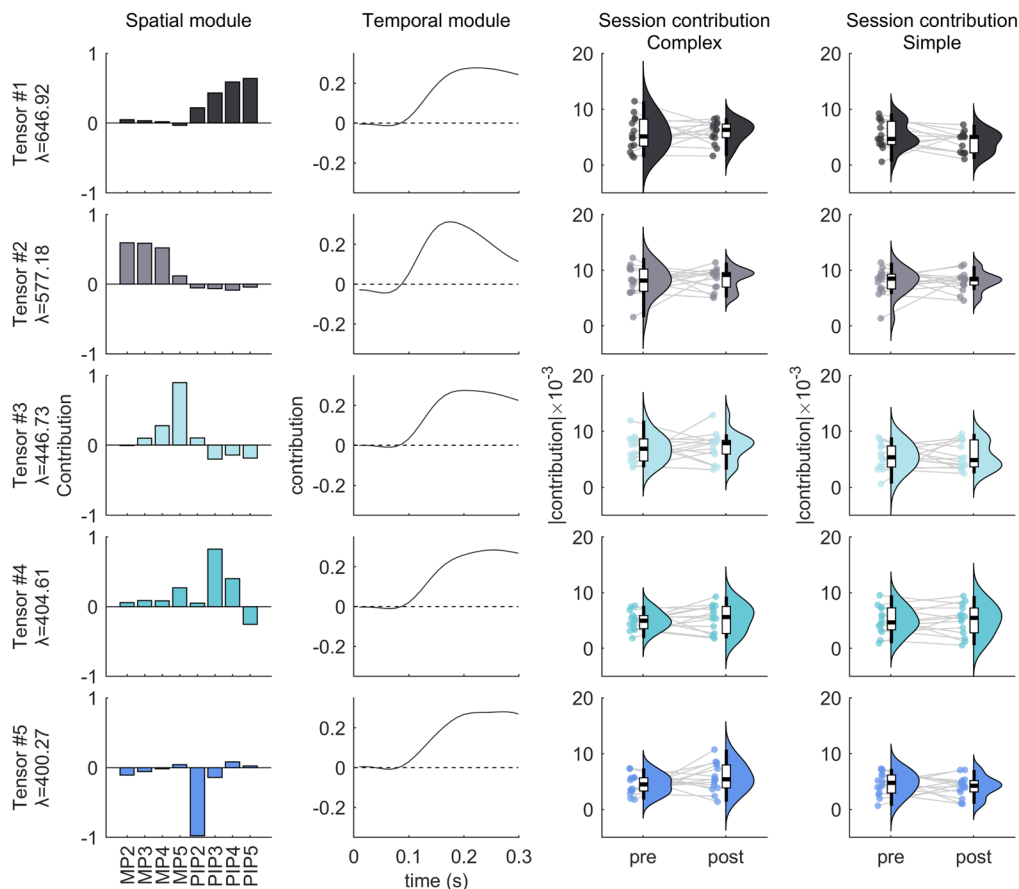


Fig. 5. Results of patterns of the left finger movements evoked by TMS over the right primary motor cortex.

motor skill improvement. These findings indicate the effect of the passive training specifically on the trained motor skill but not on general sensorimotor functions, although we cannot rule out the possibility that some sensorimotor functions that were not evaluated in the present study were improved with the training. One candidate mechanism based on our results is the increased involvement of the modules representing the individuated finger movements in performance of the trained motor skill. We found that patterns of multifinger movements evoked by TMS over the left motor cortex were changed at the trained right hand specifically after the passive training of the complex finger movements with the exoskeleton. The change accompanied increased involvement of constituent movement elements characterizing the individuated finger movements. This movement reorganization indicates neuroplastic adaptation of the corticospinal system (39). Previous studies reported that stimulation of the somatosensory neurons activated neurons in the motor cortex (40), which indicates the functional connectivity between the somatosensory and motor areas. This connectivity may underlie the reorganization of movements encoded in the corticospinal system through the passive movements.

Another possible mechanism underlying the training effect is the updating of the sensorimotor planning that guides fast performance of the complex multifinger movements. We found that passive training with the complex motion yielded nonuniform alteration of muscular coordination patterns, being characterized by earlier and smaller muscular activities. This alteration may reflect facilitation of efficient neuromuscular control, which is compatible with previous findings that have demonstrated association of the shorter duration of muscular bursts and reduced activation of muscles that are not involved in task performance with faster piano performance (15, 41). Reorganization of muscular coordination has been reported through training with voluntary movements (15, 42) and development of movement disorders through overtraining (36, 43). However, no study has demonstrated reshaping of muscular coordination patterns via sensory training without voluntary motions. This suggests that somatosensory information representing the target motor skill updated the sensory target that guides the movements toward one associated with the target skill, which has been reported to be encoded in the somatosensory cortex (44). Because somatosensory signals from one hand are encoded not only in the contralateral somatosensory region but also in the ipsilateral region via a corpus callosum (45), passive training may update the sensory target of movements with the trained and untrained hands. This putative neuroplastic change may provide an explanation for our observation of the intermanual transfer effect of the passive training without training-related changes in the TMS-induced movements at the untrained hand. The motor skill improvement induced by the present training was statistically significantly but weakly correlated between the trained and untrained hands ($r = 0.57$, $P = 0.03$), which does not reject either of the two aforementioned mechanisms. Because the present study was not originally designed to elucidate the mechanisms underlying the improved motor skill through passive training, future studies are necessary. One may also postulate that the refined motor program provided more precise error information between the desired and produced movements and thereby improved the motor skill via feedback error learning on the basis of previous findings highlighting the importance of somatosensory functions in motor adaptation (17, 46). However, this is unlikely given that the training effect was observed immediately after training and was not enhanced through repetition of the keystrokes during the posttest session. Our findings suggest that the bottleneck for

surmounting the ceiling effect of overtrained complex motor skills is the lack of prior sensory experience with them until they were learned, which can be overcome by leveraging the exoskeleton robot that generates fast, complex movements.

In contrast with the trained right hand, the untrained left hand showed no change in the patterns of multifinger movements evoked by stimulation over the right motor cortex after the passive training. This indicates that the improved motor skill of the untrained hand (i.e., the intermanual transfer effect of motor learning) was not associated with neuroplastic adaptation of the corticospinal system. In addition to the aforementioned possibility (update of sensory targets guiding movements), another potential explanation for it is that the other motor-related regions play a role in the intermanual transfer. For example, previous studies demonstrated that the supplementary motor area is responsible for intermanual transfer (47). Because the present study is not designed to address this issue, future studies are needed.

The proposed hand robotic exoskeleton has several unique features compared with previously developed exoskeleton robots and exosuits. Although previous robotic exoskeletons have primarily focused on assisting limb movements (33, 34), stabilizing body posture (30), and facilitating daily manual skills such as grasping (25), the present hand exoskeleton was uniquely tailored for fast and independent control of multifinger movements. In this respect, the proposed exoskeleton stands apart from hand robotic exoskeletons designed for haptic interactions in virtual environments, because our proposed robot can generate fast and precise flexion and extension movements of the individual fingers for a prolonged period. Accommodating speed and durability of dexterous finger movements is a unique feature of the present hand exoskeleton compared with others, such as a soft exoskeleton that can move fast but not stably for a prolonged period (48). This feature is made possible by the remote center of motion (RCM) mechanism of the present exoskeleton that forms a closed link (fig. S3), in contrast with existing hand exoskeleton robots that fail to produce spatially accurate finger motions when moving quickly and repetitively without placing stress on the user's fingers. One may also consider that the wire link mechanism can generate fast and accurate finger motions bidirectionally, but it does not guarantee consistent production of the target motion, with reduced mechanical loss due to deflection, friction, and deformation, which makes it difficult to use for a prolonged period. Furthermore, in contrast with previous robotic exoskeletons designed to be worn on the body to augment motor performance, the proposed robot was specifically engineered to improve motor skills without needing to be attached to the body during motor performance. Thus, this device is not intended to assist in movements but to induce neuroplastic adaptation. The proposed hand exoskeleton robot has diverse application prospects, including rehabilitation of neurological disorders that degrade manual dexterity and the haptic transfer of complex motor skills from teachers to students.

One potential limitation of the present study is that it remains unclear why the observed improvement of the target motor skill was not achieved by alternate forms of voluntary practicing. The rate of voluntary keystrokes at home and in the laboratory was lower than the maximum rate of the keystrokes to minimize the risk of inducing muscular fatigue through practicing. It is therefore not known whether practicing at the maximum rate of keystrokes with some rest can further improve the maximum rate of voluntary keystrokes. In study 3, although we repeated each of the pretest and posttest

sessions over five trials in which the pianists played at the maximum rate, there was no improvement in performance across trials. This further indicates that such a short-term repetition of the fastest key-strokes can yield no learning. However, our preliminary investigation found it difficult to continue to play at the maximum rate for more than 10 s and to play it for more than 10 trials repetitively, which should be carefully taken into consideration when designing a future study to evaluate effects of repetitive practicing of key-strokes at the maximum rate.

In conclusion, the present study provided evidence that passive exposure to fast and complex motions with no prior experience enables enhancement of the already well-honed skills of experts and overcoming the limits of motor expertise. This highlights the importance of embodying otherwise impossible skills using augmentation technology such as a robotic exoskeleton. The effect of passive training accompanied neuroplastic adaptation of the corticospinal system such that the somatosensory afferent signals could reorganize the encoded patterns of multifinger movements.

MATERIALS AND METHODS

The present study consisted of three studies and evaluated the effects of different sets of intervention through a comparison between behavioral and neurophysiological assessments before and after the intervention (fig. S4). Study 1 tested whether passive training with the exoskeleton could overcome the ceiling effect of the motor expertise of expert pianists. Study 2 was designed to identify the effects of different sets of passive training on the performance of different motor tasks. Study 3 assessed neuroplastic changes in the corticospinal system via TMS over the motor cortex through the passive training.

Participants

The present research consisted of three studies, in which 30 (24 females, 22.6 ± 4.2 years old), 60 (54 females, 23.1 ± 5.0 years old), and 28 (23 females, 25.2 ± 5.8 years old) right-handed pianists with no history of neurological disorders participated in studies 1, 2, and 3, respectively. All of the pianists majored in piano performance at a musical conservatory and had extensive and continuous private piano training under the supervision of a professional pianist/piano professor. Inclusion criteria were that participants had started playing the piano before 8 years old and that the total amount of piano practice until the age of 20 was more than 10,000 hours, which confirmed their experience of deliberate piano practice. In accordance with the Declaration of Helsinki, the experimental procedures were explained to all participants. Informed consent was obtained from all participants before participating in the experiment, and the experimental protocol was approved by the ethics committee of Sony Corporation (approval no. 20-14-0001).

Experimental design

Study 1

The first study consisted of two experiments, which were performed both at home and at the laboratory in succession. Before performing the laboratory-based experiment, participants were asked to practice a designated motor task with the piano at home every day for 2 weeks. The task was characterized by alternate repetition of simultaneous strikes of every other key (D and F keys) with the right index and ring fingers and simultaneous strikes of their adjacent

keys (E and G keys) with the right middle and little fingers (Fig. 1B). In other words, this chord-trill task involved repetition of two sets of simultaneous strikes of the two keys while leaving one white key in between (i.e., major third interval), using the right index and ring fingers for one set and the right middle and little fingers for another set, at a predetermined loudness (*mezzo forte*). We used this task because it has been widely recognized as technically challenging to play such a chord-trill task, which appears in various musical pieces (e.g., Étude Op. 25, No. 6 by Frederik Chopin, Ondine by Maurice Ravel, and the first movement of Piano Sonata No. 3 by Ludwig van Beethoven), quickly and accurately. In the practice session, piano practice was performed at a tempo of 80 beats per minute (BPM) for 10 s, followed by a rest period for 10 s. In the morning and afternoon every day, 30 practice sessions were performed (for about 10 min). On the 1st, 5th, 10th, and 14th days in the home-based experiment, the performance, in which the participants performed the designated keystroke task twice with the piano as quickly and accurately as possible, was assessed, and the time-varying vertical position data of the keys to be struck were recorded and stored by a customized sensing system that we developed (49).

On the day after the 2-week practice at home, the pianists were asked to participate in the experiment at the laboratory, which consisted of the pretest, training, and posttest sessions. In the training session, participants were randomly assigned into two groups and underwent different passive somatosensory training sessions. The four fingers were passively moved using a hand exoskeleton robot, and the movement pattern of these fingers differed between the two groups (complex and simple movement patterns; Fig. 1C inset, right). The complex movement pattern was characterized by alternating repetition of simultaneous flexion of the index and ring fingers with simultaneous extension of the middle and little fingers and vice versa (the same as the designated keystroke task) (movie S1). Training with a simple movement pattern was performed as a control condition, in which simultaneous flexion and extension of all four fingers was repeated, similar to grasping. For both movement patterns, the rate of the passive finger movements was four cycles of flexion and extension per second, which was faster than the maximum rate of keystrokes with the complex pattern among the present participants (on average, 2.3 strikes per second). During the training, participants kept their eyes closed and their forearm and wrist on the armrest so that they did not have to hold the exoskeleton robot voluntarily. While the fingers were being moved by the exoskeleton robot, muscular activities were monitored online using surface electromyography (EMG) to confirm no reflex-like and/or tonic muscular contractions throughout the training session. To further verify that the intervention with the exoskeleton was performed passively, we also performed an experiment to assess whether the passive exposure to the fast and complex multifinger movements did not accompany the muscular contraction. The activity of the FDS muscle was recorded from another nine pianists during 10 min of exposure to complex finger movements at a rate of 4 Hz with the exoskeleton. The data were low-pass-filtered with the Butterworth filter with a cutoff frequency of 24 Hz, root mean squared, averaged across time during the period when the exoskeleton was moving the fingers, and divided by the maximum voluntary contraction (MVC) value recorded before the intervention session for each participant (see details of the MVC procedure and analyses below). The confidence interval of the normalized muscular activity averaged during the period when the fingers were

moved passively was from 1.3 to 5.8% MVC, whereas that at rest (i.e., background EMG) was from 1.1 to 4.0% MVC. A paired *t* test confirmed no significant difference in the muscular activity between being moved by the exoskeleton and at rest [$t(9) = -1.923$, $P = 0.087$]. This confirmed that the intervention was done in a passive manner.

Before and after the training session, the pretest and posttest sessions were performed. In addition, a retention session was included 30 min after the first posttest session (termed posttest 2). During these test sessions, the motor skill was assessed by asking the participants to perform the designated keystroke task with the piano for 5 s twice, as quickly and accurately as possible. One day after the laboratory-based experiment, the motor skill of the participants was assessed at home using the designated piano task, and the keystrokes were recorded by the sensing system to evaluate the 1-day retention effect of the passive somatosensory training.

In addition to assessing the motor skills related to piano keystrokes, somatosensory and motor functions and anatomical features of the fingers were assessed in the pretest and posttest sessions. The strength of the individual digits was assessed by asking the participants to exert the maximum flexion force in an isometric manner with each of the digits of the right hand for 3 s. The movement independence of the individual digits was assessed by having the participants exert a flexion force with 50% of the maximum finger strength for 3 s with one digit while the other digits were placed on the force sensors to measure the spillover effect of the single-finger force production on the adjacent fingers (50, 51). The maximum rate of fast repetitive finger movements as an index of movement agility was assessed by asking the participants to repetitively tap the force sensor with each of the digits of the right hand as quickly and accurately as possible while keeping the remaining digits immobilized for 5 s (50). The maximum range of movements of each finger for both flexion and extension directions was assessed by having each finger passively stretched to the anatomical limit by an experimenter. We used an inertial measurement unit sensor attached to both the proximal phalanx and metacarpal bone of each finger to measure the range of motion. The somatosensory function of movement speed perception was evaluated using a movement speed discrimination task to identify the perception threshold of the movement speed between a pair of fingers. The index and ring fingers were rotated for flexion within the range of motion of 45° with different movement durations by the hand exoskeleton robot, and the threshold of perception of movement speed was identified by adjusting the movement duration with a staircase method in steps of 10 ms. The movement durations of the index and ring finger in the first trial were set to 300 and 40 ms, respectively, and the movement duration of the index finger in the next trial was decreased or increased by 10 ms, depending on whether correct answers were repeated three times or an answer was incorrect once, respectively (a three-down one-up staircase method). The test was finished when four peaks and four troughs were recorded. We defined the average value of the last two peaks and two troughs of the speed as the perceptual threshold of the movement-speed discrimination.

Study 2

The second study was designed to identify what elements of movements in training are responsible for enhancement of motor skills. The study consisted of the pretest, intervention, and posttest sessions, and 60 pianists were randomly assigned into five groups with different interventions. In two groups, the participants underwent

passive motion training with a complex movement pattern at two different movement rates (four cycles and one cycle of flexion and extension per second, respectively). In another group, the participants underwent passive motion training with a simple grasping-like movement pattern at a movement rate of four cycles of flexion and extension per second. In the active control group, the participants were asked to actively perform the designated piano keystroke task at a rate of two keystrokes per second. They took a rest for 10 s every minute of the performance. In the passive control group, the participants took a rest for 30 min. For all groups, the intervention session was 30 min.

In the pretest and posttest sessions in study 2, the participants were asked to perform three piano-keystroke tasks. The first task involved alternate repetition of simultaneous strikes of every other piano key (D and F keys) with the index and ring fingers and simultaneous strikes of their adjacent keys (E and G keys) with the middle and little fingers as quickly and accurately as possible. The second task was a mirrored version of the first task with the same fingering, which was performed with the left hand (the hand without any intervention) to assess the intermanual transfer effect of the passive training performed with the right hand. The third task involved repeating simultaneous strikes of four adjacent keys (D, E, F, and G keys) with the right index, middle, ring, and little fingers, respectively, as quickly and accurately as possible. These tasks were performed for 5 s in each of the three successive trials.

Study 3

The third study was designed to assess neuroplastic changes in the corticospinal system throughout the passive training. The experiment consisted of the pretest, training, and posttest sessions. The training session was performed in the same manner as the laboratory-based experiment of the first study. Twenty-eight pianists were randomly assigned into two groups who underwent different passive somatosensory training (i.e., complex and simple movement patterns at the rate of four cycles of flexion and extension per second for 30 min). For the pretest and posttest sessions, both the behavioral and neurophysiological assessments were performed. In the behavioral assessment, the participants performed the fastest keystroke task involving the complex pattern of multifinger movements with the piano for 5 s. The task was performed five times with each hand. In the neurophysiological assessment, we recorded the finger movements evoked by TMS over each of the right and left primary motor cortices (M1). We used a figure-of-eight coil connected to a Magstim 200 stimulator. To define the location of the stimulation, we recorded electromyographic activity from the FDS muscle. EMG activity was recorded with Ag/AgCl disposal electrodes. Standard skin preparation was performed before attachment of the electrodes. The electrodes were mounted over the muscle belly in a bipolar montage. The signals were amplified, band-pass-filtered (10 to 1 kHz), and sampled at 2 kHz (PowerLab, ADInstruments). We determined the optimal position for evoking motor-evoked potentials (MEPs) from the FDS and marked it on a swimming cap worn by each participant. We then marked 24 stimulation sites around the optimal position (the hot spot) in 1-cm steps (see Fig. 4A). The resting motor threshold was defined as the lowest intensity that evoked an MEP of 50 μ V in 5 of 10 trials at the hot spot. The resting motor thresholds in the groups undergoing the complex and simple movements were $43.1 \pm 6.9\%$ and $39.2 \pm 5.6\%$ of the maximum stimulator output for the right hand, respectively, and $39.2 \pm 5.6\%$ and $42.5 \pm 5.4\%$ of the maximum stimulator output for the left hand, respectively.

Finger movements evoked by TMS were recorded with a data glove (CyberGlove II; CyberGlove Systems) with a custom-made script of LabView. We recorded the joint angle with an angular resolution of $<0.5^\circ$, with a sampling frequency of 90 Hz. Each participant wore the data glove on the hand contralateral to the stimulated cortex. The participants kept the hand in a pronated position with their forearm on the armrest. Data were sampled from the PIP joints and MP joints of the index, middle, ring, and little fingers.

To evoke the finger movements by TMS, we stimulated the right and left M1 at an intensity 1.6 times higher than the resting motor threshold. This intensity was chosen because coordinated finger movements were not evoked by lower intensities. The TMS coil was fixed tangentially to the scalp with the handle pointing backward and rotated approximately 45° away from the midsagittal line. Ten TMS pulses were applied to each of the 25 stimulation sites in a randomized order. Therefore, a total of 250 finger joint movements were recorded (25 sites, 10 pulses) with each hand during the pretest and posttest sessions. We stimulated the M1 every 5 s. The finger kinematics was recorded from 100 ms before to 400 ms after the stimulation. The TMS-evoked finger movements were represented by a matrix of the time-varying joint angles, which consists of the angles of eight joints over the recorded time window.

Experimental apparatus and data acquisition

In the present study, a custom-made motor-driven hand exoskeleton robot was used to apply force to the proximal phalange of each of the four fingers and to flex and extend the MP joint of each finger with an angular resolution of less than 1.0° (Fig. 1A). We did not attach the exoskeleton on the middle phalange because the force applied by the exoskeleton rotates both the MP and PIP joints, and the amount of the rotation varies across the individuals. The robot moves in a manner designated in a predefined text file that delineates a sequence of joint angles of the fingers over time with a temporal resolution of 10 ms. Details of the control system of the exoskeleton are illustrated in fig. S5. Before beginning the experiment, we assessed the functionality of the exoskeleton robot. The verification process confirmed that the robot could reliably execute bidirectional finger movements, encompassing a range of motion of 50° , at a movement rate of 4 Hz for a duration of 30 min, safely by keeping the temperature of the robot under 28°C , which has not been ensured by any commercialized exoskeleton robots. This functionality was ensured when the servo motor (RS303MR, Futaba Co.) was supplied with a consistent voltage of 5 V. Our exoskeleton robot used the RCM mechanism that enables generation of the target force on the finger accurately while minimizing mechanical stress on the surface of the finger through repetitive motions, in contrast with the serial link mechanism that conventional hand exoskeleton robots have used (fig. S3).

In the laboratory-based experiment, we used an acoustic upright piano with musical instrument digital interface (MIDI) sensors (YAMAHA Co., Japan). The timing and velocity of the individual key presses (i.e., onset of the keystrokes) and key releases were recorded using our custom-made script (temporal resolution = 2 ms). On the basis of this information, the IKI was computed as a difference in timing between two successive keypresses. In the home-based experiment in study 1, we used a custom-made contactless optical sensor system that can be mounted on the piano keys without interfering with the mechanical actions of the keys. This sensing system can record the time-varying vertical positions of

eight adjacent piano keys (one octave) with a temporal resolution of 1 ms (49). The data recorded by the sensors were stored in a micro-computer (Raspberry Pi 4). The sensing system was delivered to the 30 pianists, and after the data collection process, the system was returned to the laboratory for offline analyses of the collected data.

In study 1, surface EMG with active electrodes (Trigno mini, Delsys Co., USA) was used to measure the activity of the seven intrinsic and extrinsic finger muscles [the first, second, third, and fourth dorsal interosseous (1DI, 2DI, 3DI, and 4DI); ADM; FDS; and extensor digitorum communis] of the right hand via an analog-digital board (NI USB-6363, National Instruments Co., USA) in synchronization with the data measurement of the vertical position of piano keys (MIDI). Here, the online synchronization of data measurement of EMG and MIDI information was performed using a custom-made script of LabView. Each electrode was mounted over the muscle belly. Before the experiment, we carefully checked that each electrode recorded the activity of each of the muscles without any cross-talk by asking each participant to exert isometric force with each finger. The EMG signals were amplified, band-pass-filtered (10 to 500 Hz), and sampled at 1 kHz using Data Acquisition Toolbox with MATLAB (MathWorks Co., USA). Before initiating the experiment, MVC was performed so that all fingers exerted isometric force in an MVC manner for both flexion and extension against the experimenter's hand placed on the participant's fingers for 3 s. This MVC measurement session was repeated twice, and the average across trials was used as a representative of the MVC.

Data analysis

The IKI was computed as the difference in the timing of the keypress between two successive strikes of the same key, which was then averaged across the keypresses within a trial. The derived mean IKI within a trial was averaged among the trials for the pretest, posttest, and retention sessions to assess any interventional effects on the fastest piano performance in the individual tasks. In addition, the temporal precision of the keystrokes was also evaluated by computing the absolute value of the temporal gap between the moments of two simultaneous keystrokes in the chord-trill task (i.e., between the index and ring finger keystrokes and between the middle and little finger keystrokes). The timing error of the two simultaneous keystrokes was then averaged across strikes for each participant, which was used to assess the speed-accuracy trade-off.

In the home-based experiment in study 1, the vertical position data of the keys were low-pass-filtered using a second-order Butterworth filter with a cutoff frequency of 24 Hz. The moment when the individual keystroke was performed was computed to assess the mean IKI across strikes.

The EMG data were band-pass-filtered with a cutoff frequency between 10 and 250 Hz to remove movement artifacts and high-frequency noise, full-wave-rectified, and time-normalized so that each IKI between two successive strikes with the index finger consisted of 1000 time points. Time normalization was performed so that the data could be compared among the sessions and participants. The median of the preprocessed time-varying EMG data across the trials was computed to ensure that the data were robust against occasional high-amplitude spikes arising from noise (43), which was inevitable because of the fast and complex changes in hand configuration while playing the piano. The EMG data after the aforementioned pre-processing were normalized in amplitude according to the MVC value, which was defined as the mean of the maximum values of the

preprocessed EMG data (the aforementioned preprocessing including the filtering and rectification) during MVC measurement across the two trials.

The normalized EMG data were analyzed using the NMF algorithm (52) to identify a set of patterns of simultaneous activation across the muscles. The NMF decomposed the EMG waveforms of the seven intrinsic and extrinsic finger muscles into a set of NMF factors that consisted of time-varying waveforms (“feature score”) and coefficient vectors representing the activation of the synergy score for the individual muscles (“feature vector”) (Fig. 3, B and C). The NMF algorithm requires specification of the number of factors to be extracted a priori. We manipulated the number of NMF factors from one to seven for each EMG dataset and calculated the variance accounted for at each number of NMF factors. The number of NMF factors used for further analyses was determined so that the factors could account for more than 90% of the total variance. The results showed that the variance accounted for by two factors derived from NMF was $91.9 \pm 3.7\%$ (mean \pm SD across participants). We therefore chose the two NMF factors for subsequent analyses. An inner product between the two feature vectors of the extracted NMF factors was computed to sort the two NMF factors across sessions and participants, such that one feature score matched one with the peak waveform appearing at the moment of the simultaneous strikes with the index and ring fingers (i.e., normalized time points of 0 and 100), and another feature score matched one with the peak waveform at the moment of the strikes with the middle and little fingers (i.e., normalized time point of 50) (Fig. 3C).

The recorded finger kinematic data were first preprocessed with offset correction on the basis of the mean of the values obtained before the stimulation and low-pass filtering by the fourth-order Butterworth filter with a cutoff frequency of 10 Hz. Thus, positive and negative values indicate flexion and extension relative to the finger posture at rest, respectively. The waveforms during the period from the onset of the stimulation to 300 ms after it were used for the subsequent analyses. To extract a set of coordinated patterns of movements across joints, the preprocessed kinematic data of all participants were analyzed by tensor decomposition. The analyses were performed in the same manner as a previous study (38) using the tensor toolbox (<https://tensortoolbox.org>) in MATLAB (MathWorks Co.). Briefly, the input data into tensor composition were arranged in three-dimensional arrays, in which each array consisted of joints, time points, and a concatenation of participants, trials, and sessions. We standardized the joint angles such that the mean and SD of each joint for each participant across all trials and sessions were 0 and 1, respectively. This enabled us to compare among different joints, sessions, and participants appropriately. The output of tensor decomposition consisted of joints (spatial modules), time points (temporal modules), and trials for each component. A spatial module described a group of joints that covary in motion, whereas its associated temporal module represented the time-varying movement pattern common within each spatial module. The array of trials was classified according to session (pretest and posttest) and participants (two groups). This movement decomposition is associated with the concept of movement synergies (35, 53) but extends it by taking into account variance of movements across the individuals. The extracted spatial and temporal modules were averaged across participants within each of the two groups who underwent different passive training to evaluate their group differences. Tensors were aligned according to the extent to which each extracted

module accounted for the original finger movements [i.e., λ (38)]. Tensor decomposition was performed for each hand.

Statistics

For study 1, our primary hypothesis was that effects of the passive movement training on the motor performance differ according to the pattern of the multifinger movements during the training (i.e., group-wise differences). To test it, a two-way mixed-design ANOVA using the group (passive training with complex and simple motions) and session (tests before and after the training) was performed for the mean IKI value across strikes and the features derived from the EMG analyses. Only for the weighting coefficients of the NMF results, to test the hypothesis that groupwise differences in training effects vary across muscles, was a three-way mixed-design ANOVA performed using the group, session, and muscle as independent variables. We also tested another hypothesis of no difference in the training effect between the fingers by performing a linear mixed model analysis using the fingers (four levels: index, middle, ring, and little fingers) and group (two levels: passive training with complex and simple motions) as fixed effects for the differential value of the IKI between the pretest and posttest sessions. Furthermore, to test a hypothesis of training effects on sensorimotor functions and anatomical features of the fingers, we developed a linear mixed model using the group and session as fixed effects and finger and participant as random effects.

For study 2, our hypothesis was that there would be groupwise differences in the training effect on motor performance. To test it, a two-way mixed-design ANOVA using group (five different sets of interventions) and session (pretest and posttest) was performed on the IKI of the right hand. This test was also performed on the IKI of the left hand to test the intermanual transfer effect of training.

For study 3, we hypothesized that changes in patterns of the TMS-evoked finger movements through training differ according to the movement patterns used for the training. This hypothesis was tested using a linear mixed model with the group (training with the complex and simple movements), session (pretest and posttest), and component as independent variables and participant, participant*session, and participant*component as random effects for the contribution of each component derived from tensor decomposition. Mauchly's test was used to test for sphericity before performing each ANOVA, and for nonspherical data, Greenhouse-Geisser correction was performed. Post hoc tests with the Benjamini-Hochberg correction for multiple comparisons were performed in the case of significance. These statistical analyses were performed with R statistical software (ver. 3.2.3.).

Supplementary Materials

The PDF file includes:

Figs. S1 to S5

Tables S1 to S7

Legends for movies S1 to S3

Other Supplementary Material for this manuscript includes the following:

Movies S1 to S3

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