ACQUISITION OF INDIVIDUATED FINGER MOVEMENTS THROUGH MUSICAL PRACTICE

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Abstract—Individuated finger movements represent a key feature of hand dexterity. However, our understanding of mechanisms underlying the acquisition of this motor skill is limited. The present study aimed to identify the effects of daily motor training on acquisition of individuated finger movements. Ten musically naïve individuals performed piano practice for 4 successive days, and hand kinematics were evaluated using a motion capture system. The results showed a decrease in movement covariation across fingers with practice, particularly at the ring and little fingers. The decrease was more pronounced in the pair of fingers with lower independent control prior to the practice. Furthermore, a few finger pairs demonstrated facilitated movement independence when the subject was provided with visual feedback (VFB) regarding the rhythmic accuracy of motor actions following each practice. The results provide evidence for the enhancement of individuated finger movements through dexterous hand use during piano practice, which suggests plastic adaptation of the neuromuscular system associated with independent control of finger movement. © 2014 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: motor learning, neuroplasticity, fine motor control, motor skill, hand dexterity.

INTRODUCTION

The neuromuscular architecture of the hand constrains the independent control of individual finger movements. The constraint includes the anatomical linkages between the tendons and muscles of the hand (Leijnse et al., 1993; Lang and Schieber, 2004a), the synchronous firing of motor neurons innervating into adjacent finger

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muscles (Kilbreath and Gandevia, 1994; Keen and Fuglevand, 2004; Winges et al., 2008), and the shared representation of individual fingers in the motor cortex (Schieber and Hibbard, 1993; Sanes et al., 1995), Consequently, the motion of a single finger yields a covariation of motion at the adjacent fingers (Häger-Ross and Schieber, 2000). This movement covariation may simplify the control of relatively simple hand movements such as grasping (Santello et al., 1998, 2002;Mason et al., 2001; Gentner and Classen, 2006) and haptic exploration (Thakur et al., 2008) by reducing the dimensionality of the control of multiple joints/muscles in the hand (Overduin et al., 2012; Santello et al., 2013). However, dexterous hand use, which represents skilled motor behavior, requires moving multiple fingers in an opposite direction, or even independently, against these neuromuscular constraints. This motor skill is sometimes impaired through development of overtraining-induced neurological disorders such as focal dystonia (Curra et al., 2004; Sohn and Hallett, 2004; Rosenkranz et al., 2009; Furuya and Altenmüller, 2013), which implicates its association with neuroplasticity. Of particular importance is an understanding of the neuroplastic mechanisms subserving the individuated finger movements, which may not only shed light on acquisition and loss of hand dexterity, but also aid in designing an optimal program for facilitating fine motor control for unskilled and elderly individuals (Shim et al., 2004) and for patients with movement disorders that exacerbate dexterous hand use (Lang and Schieber, 2004a; Raghavan et al., 2006; Brandauer et al., 2012; Park et al., 2012).

Previous studies that compared repetitive finger movements between musicians and non-musicians using a cross-sectional design demonstrated enhancement of individuated finger movements in musicians (Parlitz et al., 1998; Slobounov et al., 2002; Aoki et al., 2005). A recent study also demonstrated the equal independence of movements across fingers in expert pianists (Furuya et al., 2011a) over a wide range of movement rates (Furuya and Soechting, 2012), which differed from the findings in musically untrained individuals (Häger-Ross and Schieber, 2000; Zatsiorsky et al., 2000; van Duinen and Gandevia, 2011). These findings suggest the acquisition of this motor skill through extensive training, presumably through plastic neuromuscular adaptations (Jäncke, 2009). However, several confounding factors remain, such as the genetic predisposition of neuromuscular anatomy and function and the explicit instruction provided through music education. A longitudinal study would serve for

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[†] These authors contributed equally and are co-first authors. *Abbreviations:* DIP, distal-interphalangeal; IKI, inter-keystroke interval; MCP, metacarpophalangeal; NFB, normal feedback; PIP, proximalinterphalangeal; ROM, range of motion; VFB, visual feedback.

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better understanding whether the superior independent control of finger movements in musicians is a product of nature or nurture (Wan and Schlaug, 2010).

Piano performance provides a rich and natural environment that requires independent finger control such as a precisely timed strike and release of keys in succession with multiple fingers (Furuya et al., 2011a). The spontaneous covariation of movements across fingers may elicit unwanted tones and/or distorted rhythm and articulation. Thus, a mastery of piano playing should accompany skill acquisition for moving fingers independently. In addition to extensive piano practice, specific instruction in piano can play a role in the acquisition of independent control of finger movements. For example, during motor training of the independent control of static force production in fingers, visual feedback (VFB) regarding the motor performance facilitated independent finger control (Chiang et al., 2004). This result suggests the importance of providing extrinsic information on movement accuracy for acquiring this skill. Since perceptual abilities that are also not well fine-tuned in untrained individuals as compared to musicians (Kraus and Chandrasekaran, 2010) may make it difficult to gain precise information on movement error, extrinsic VFB may aid in facilitating feedback error learning (Kawato, 1999). Indeed, motor skill acquisition with explicit VFB activates distinct neural networks (Debaere et al., 2003; Ronsse et al., 2011).

The primary goal of the study was to identify the effects of daily musical training on individuated finger movements. Based on the previous findings of lower independent movement control in the middle and ring fingers compared with the index and little fingers for the untrained non-musicians (Häger-Ross and Schieber, 2000; Zatsiorsky et al., 2000) but not for the expert pianists (Furuya et al., 2011a), we hypothesized a larger learning gain at the fingers with potentially low independent control. It was also postulated that joints with a larger range of motion (ROM) would display a greater learning effect. We also assessed the effect of practicing with provision of VFB regarding the rhythmic accuracy of motor actions on individuated finger movements. We hypothesized improvements in independent finger control following musical training and its facilitation through providing explicit VFB.

EXPERIMENTAL PROCEDURES

Participants

Ten musically naïve adult individuals were randomly assigned to two groups. One group (one female, four males; age: 21–24 yrs) was provided explicit VFB regarding the rhythmic accuracy of movements (i.e., VFB) following each practice trial (VFB group). The age-matched control group (five males; age: 21–24 yrs) did not receive any explicit VFB regarding performance (normal feedback (NFB), group). All participants were right-handed, with a laterality index of 89.1 ± 8.1 (all > 80) (Oldfield, 1971). All participants had neither formal education in playing musical instruments prior to the experiment nor other expertise requiring dexterous use

of the hand (e.g. sewing, painting). The experimental protocol was approved by the local ethics board of Kwansei Gakuin University, and all participants provided informed consent prior to the experiment. The experiment was performed according to the Declaration of Helsinki.

Experimental design

The experiment consisted of 50 practice trials for 4 successive days (200 trials in total). During the practice, each participant played a certain tone sequence consisting of 12 strokes with a predetermined fingering that used all possible finger pairs of the left hand (Fig. 1A). In each trial, the four fingers were used three times. The index, middle, ring, and little finger always struck a key of F, E, D, and C, respectively. The thumb was not included because our previous study demonstrated different movement patterns between the thumb and the fingers (Furuya et al., 2011a). We chose the non-dominant left hand because this hand is less frequently used in daily and sports activities compared with the dominant hand. The participant played a digital piano (YAMAHA, P-250) with an inter-keystroke interval (IKI) of 500 ms in synchronization with a metronome (two strokes per second) at a predetermined speed with which each key was depressed (90-MIDI velocity; note that MIDI velocities provided by the interface range from 1 to 127). This task was repeated 50 times per day, among which the first five and last five trials were used to record and assess the hand kinematics (Fig. 1B). During the



Fig. 1. (A) The practice task on musical score. The number below each note specifies the fingering (2, 3, 4, and 5 correspond to the index, middle, ring, and little fingers, respectively). (B) The experimental flow. Each day of training consisted of 50 practice trials. The initial and final five trials were used for analysis, defined as the pretraining and post-training sessions, respectively. (C) Visual feedback on rhythmic accuracy of keystrokes during one previous (left bar) and current (right bar) trials. The plot was visually presented on a PC monitor located in front of a participant after each trial only for the VFB group.

task, the trunk was in an upright position with no movement while the right arm and hand were kept relaxed and placed on the side of the trunk. The left upper-arm and forearm was perpendicular and horizontal to the ground, respectively.

Prior to data recording on the first day, each participant in both the VFB and NFB groups was allowed to practice to familiarize themselves with both the given tone sequence and the piano by accepting instructions from the experimenter, which took approximately 5 min. All participants memorized the sequence and fingering during the familiarization session so that they could play without errors.

Data measurement and analysis

Provision of VFB regarding rhythmic accuracy of movements. In order to explicitly provide only VFB group with VFB regarding a specific variable regarding how precisely the player kept the timing of successive keystrokes, MIDI data were collected during the experiment from the piano using a custom-made script written in JAVA with a time resolution of 1 ms. This script allowed us to record the time at which each key was depressed and released and to compute the IKI as the interval from key depression to key depression. To provide VFB regarding movement accuracy explicitly, the rhythmic error, defined as $\sum_{i=1}^{11} |IKI_i - 500|/11$ (i indicates the intervals between successive key strokes), was computed as an index of rhythmic inaccuracy during each trial only in the VFB group. Here, the subtracted number from IKI (i.e. 500 ms) represents ideal performance given a target speed of 2 Hz. Note that this error index only correctly evaluates rhythmicity at this particular playing speed. If a participant played slightly slower or faster even with perfectly regular IKIs (i.e. perfectly regular rhythm), this index would still be evaluated as an error by this formula. The computed error value was visually provided as two adjacent bar plots (Fig. 1C; left bar: one previous trial, right bar: a current trial) on a computer screen located in front of each participant following each trial.

Measurement of motion capture data. Twenty-six spherical reflective markers were mounted on the hand and forearm to identify anatomical landmarks for digitalization. These markers were placed on the skin over the fingertips and on the three joint centers of all five digits, the proximal ends of the metacarpal bones, and the distal ends of the radius and ulna (Fig. 2A). The motion of the reflective markers was recorded at 120 Hz using 13 high-speed cameras surrounding the piano (Fig. 2B). The camera locations were carefully arranged so that position data of all markers would be recorded while performing the target task. The spatial resolution in the camera setting was 1 mm. The 3D time-position data of each marker were obtained using a direct linear transformation method. All procedures were established in our previous study (Furuya et al., 2011b). The position data were digitally smoothed at a low-pass cutoff frequency of 20 Hz using a second-order Butterworth digital

filter, which aids in eliminating high-frequency noise that becomes particularly large when computing derivative values of the position data and joint angle values using a dot product.

Computation of joint angle. Using the threedimensional position data of individual markers, the flexion/extension angles at the metacarpophalangeal (MCP), proximal-interphalangeal (PIP), and distalinterphalangeal (DIP) joints were computed at the index, middle, ring, and little fingers. To compute the angle of the MCP joint of a certain finger, we used position data that consisted of four markers (Fig. 2C), including the proximal ends of this finger (marker C) and its adjacent finger (marker B), and the centers of the MCP (marker A) and PIP (marker P) joints of this finger. Here, when computing the MCP angle of the middle and ring finger, the point B corresponded to one on the ring and middle finger, respectively. A foot of a perpendicular from the point P to the plane α that contains the points A, B, and C was defined as X. The angle formed by \overrightarrow{AX} and \overrightarrow{AP} was defined as θ . Here, X is on the plane containing points A, B, and C, which yields the following equations.

$$\overrightarrow{\mathsf{PX}} = \overrightarrow{\mathsf{rPA}} + \overrightarrow{\mathsf{sPD}} + \overrightarrow{\mathsf{tPC}}$$
(1)

$$\mathbf{r} + \mathbf{s} + \mathbf{t} = \mathbf{1} \tag{2}$$

The following equations hold true because PX is orthogonal to α .

$$\overrightarrow{\mathsf{PX}} \cdot \overrightarrow{\mathsf{AB}} = 0 \tag{3}$$

$$\overrightarrow{\mathsf{PX}} \cdot \overrightarrow{\mathsf{AC}} = 0 \tag{4}$$

Because points A, B, and C are observational data, $\overrightarrow{\text{PX}}$ can be evaluated using Eqs. (1–4). Then, the vector $\overrightarrow{\text{AX}}$ was evaluated as follows.

$$\overrightarrow{\mathsf{AX}} = \overrightarrow{-\mathsf{PA}} + \overrightarrow{\mathsf{PX}} \tag{5}$$

The MCP joint angle formed by $\overrightarrow{\mathsf{AX}}$ and $\overrightarrow{\mathsf{AP}}$ (i.e., θ) was therefore evaluated as follows.

$$\theta = \arccos\left(\frac{\overrightarrow{\mathsf{AP}} \cdot \overrightarrow{\mathsf{AX}}}{\left|\overrightarrow{\mathsf{AP}}\right| \cdot \left|\overrightarrow{\mathsf{AX}}\right|}\right) * \frac{180}{\pi} \tag{6}$$

Here, it is anatomically possible that the MCP joint hyper-extends and, thus, that the value of θ exceeds π . Therefore, depending on the positional relationship between points P and X, the MCP joint angle was evaluated as follows:

$$\theta_{MCP} = \begin{cases} \pi + \theta, Py > Xy \\ \pi - \theta, Py < Xy \\ \pi, Py = Xy \end{cases}$$
(7)

where Py and Xy indicate the y-coordinate of points P and X, respectively.

The flexion/extension angle of the PIP and DIP joints, each of which has only one degree of freedom, can be computed as an inner product as follows:

$$\theta_{\mathsf{P}\mathsf{IP}} = \arccos\left(\frac{\overrightarrow{\mathsf{PA}} \cdot \overrightarrow{\mathsf{PD}}}{\left|\overrightarrow{\mathsf{PA}}\right| \cdot \left|\overrightarrow{\mathsf{PD}}\right|}\right) * \frac{180}{\pi} \tag{8}$$



Fig. 2. (A) Reflective markers on the left hand. (B) The motion capture system consisted of 13 high-speed cameras. (C) The markers used to calculate the joint angle.

$$\theta_{\mathsf{DIP}} = \arccos\left(\frac{\overrightarrow{\mathsf{DP}} \cdot \overrightarrow{\mathsf{DE}}}{|\overrightarrow{\mathsf{DP}}| \cdot |\mathsf{DE}|}\right) * \frac{180}{\pi} \tag{9}$$

where D and E are markers on the DIP joint center and the tip of the finger, respectively (Fig. 2C). Consequently, Eqs. (7–9) evaluate the flexion/extension angles of the MCP, PIP, and DIP joints, respectively, at each moment.

A time-course of angular kinematics at all joints of all fingers was time-normalized so that each IKI becomes 100 timepoints (Furuya et al., 2011a; Furuya and Soechting, 2012).

Correlation analysis. To assess the independence of movements across fingers, a correlation coefficient of the time-varying joint motion was computed between the finger used for the keystroke ("striking finger") and one of the other three fingers ("non-striking finger"). For each of the four fingers, the coefficient was computed during the period from one previous strike to one following strike with the target finger (i.e., three successive strikes). Because each trial included three strikes with each of the fingers, the coefficient was computed for each of the three strikes and then averaged. This value was averaged across the first five trials ("pre-training session") and across the final five trials ("post-training session") for each of the 4 days (Fig. 1B). The correlation coefficient was computed at the MCP, PIP, and DIP joints for each participant. To compare the coefficient value across participants, the

value (*r*) was *z*-transformed (Fisher transformation) in order to statistically compare the correlation coefficients between groups and sessions.

Rhythmic error of keystrokes. To assess movement accuracy of the individual fingers, the rhythmic error was computed for each of the four fingers based on MIDI information during the period from one previous strike to one following strike with the target finger (i.e., three successive strikes). Because each trial included three strikes with each of the fingers, the rhythmic error was computed for each of the three strikes and then averaged. This value was averaged across the first five trials ("pre-training session") and across the final five trials ("post-training session") for each of the 4 days.

Statistics

Due to the small number of participants, we performed a non-parametric permutation test using an "ezPerm" function included in a package "ez" in R (ver. 3.0.2), in order to statistically evaluate the effects of daily piano practice on the movement covariation across fingers. Independent variables included were "practice session", "finger pair", "joint" (within variable), and "group" (between variable). Here, the independent variable of "finger pair" included 12 levels (three finger pairs between the striking and non-striking fingers for each of the four striking finger). For post hoc tests for multiple



Fig. 3. A time-varying angular position of the MCP joint at the ring and little fingers in a representative participant in the NFB group (left panel), and the MCP joint at the middle and ring fingers in another representative participant in the VFB group (right panel). These finger pairs were chosen because of significant effects of session. The top and bottom panels indicate the pre-training session on the first day and the post-training session on the final day, respectively. The *x*-axis indicates the normalized time so that each strike corresponds to each tick. I, M, R, and L indicate the index, middle, ring, and little fingers, respectively.

comparisons, Wilcoxon Test was performed using a "wilcox.test" function in R. To test the hypothesis that finger pairs with potentially lower independent control yield a larger practice effect, a linear regression analysis was performed using datasets of correlation coefficients of movements across all possible finger pairs in all participants. Using the rhythmic error of keystrokes as an independent variable, we also run a non-parametric permutation test by treating "practice session", "finger" (within variables), and "group" (between variable) as dependent variables. This test was performed in order to assess whether the practice-dependent change in the rhythmic accuracy of keystrokes varies in relation to the VFB provision.

RESULTS

Time-varying angular position data

Fig. 3 illustrates the time-varying joint angular position before (upper-panel) and after (lower-panel) the 4 days

of practice with (A) and without (B) accuracy feedback in two representative individuals. The displayed finger pairs at both conditions were chosen because of the presence of significant effect of practice (see below). For striking and lifting a key, the MCP joint of the striking finger underwent a succession of extension, flexion, and extension, which formed a tri-phasic waveform. Overall, this tri-phasic pattern became more pronounced after the practice. For instance, during the initial keystroke with the ring finger for an individual in the NFB group (Fig. 3A), the little MCP joint displayed a larger extension motion at the post-training session of the final day compared to the pre-training session of the first day. This change accentuated the individuated movements of the ring and little fingers. Similarly, during the initial keystroke with the ring finger in an individual with VFB (Fig. 3B), the middle MCP joint extended more at the post-training session of the final day than at the pre-training session of the first day.

Correlation coefficients of joint motion between fingers

The group mean of the correlation coefficient of the joint angular motion between the striking and non-striking fingers was computed for the VFB and NFB groups. Table 1 summarizes the statistical results of the nonparametric permutation test using group, practice session, finger pair, and joint as independent variables. A significant three-way interaction between group, session, and finger pair was evident, which indicates that at some specific finger pairs, changes in the correlation coefficient value over practice session differed between the two groups. Fig. 4 displays the results of the finger pairs where a post hoc test identified differences between sessions or between groups (i.e. during the keystroke with either the ring or little fingers). For instance, a practice-dependent decrease in the correlation coefficient was observed only for the VFB group but not for the NFB group at the middle-ring finger pair at the MCP joint (Fig. 4A), and vice versa at the ring-little finger pair at the MCP joint (Fig. 4B) during the ring finger keystroke. In addition, there were also significant interaction effects between session and finger pair, and between group and finger pair. The former interaction indicates a different effect of practice across finger pairs (e.g. no practice-dependent change was evident only in Fig. 4D). The latter interaction indicates a group difference only at some specific finger pairs (e.g. a group effect in Fig. 4C, D but not in Fig. 4A. B).

A question then arises why only a limited number of finger pairs displayed the effect of piano practice that involves all fingers equally. To test our hypothesis whether the movement covariation prior to the piano practice was associated with the practice effect, we initially classified the group mean of the correlation coefficient into two clusters according to whether there was a significant difference between sessions (i.e., a practice effect; Fig. 5A). The right boxplot, which includes three pairs of fingers with a significant practice

 Table 1. Results of non-parametric permutation test for correlation coefficients

Effect	<i>p</i> Value
Group	0.906
Practice session	0.256
Finger pair	0.112
Joint	0.044
Group \times Practice session	0.867
Group $ imes$ Finger pair	0.013
Practice session \times Finger pair	0.015
Group \times Joint	0.327
Practice session \times Joint	0.233
Finger pair $ imes$ Joint	0.603
Group \times Practice session \times Finger pair	0.037
Group \times Practice session \times Joint	0.126
Group $ imes$ Finger pair $ imes$ Joint	0.708
Practice session \times Finger pair \times Joint	0.369
$\textbf{Group} \times \textbf{Practice session} \times \textbf{Finger pair} \times \textbf{Joint}$	0.579

A number in bold indicates p < 0.05.

effect (Fig. 4A–C), displayed higher values compared with the left boxplot, which includes the remaining coefficient values without a significant practice effect. This result indicates that the practice effect was evident for the finger pairs with low independence. To probe this idea more directly, a linear regression analysis was performed by using datasets of the correlation coefficients that pooled all finger pairs and participants in both groups at the MCP joint (Fig. 5B). There was a significant relation between the correlation coefficient at the pre-training session of the first day and the change in the correlation value following the whole practice (i.e., day 4 post-training - day 1 pre-training) at all finger pairs for all participants (Fig. 5B: p < 0.001. $R^2 = 0.28$ by a linear regression analysis). The negative correlation indicates a larger decrease in the movement covariation following the practice at the finger pair with low independence.

ROM at individual joints

To assess the amount of motion at each joint during a trial, the ROM was computed at each joint as the difference between the maximum and minimum joint angles. A non-parametric permutation test using group and session as independent variables found that neither the interaction nor the main effect of these variables. was significant at the index, middle, ring, or little fingers (p > 0.05). Thus, we averaged the ROM across sessions and groups and compared it across the MCP, PIP, and PIP joints (Fig. 6). A non-parametric permutation test confirmed a significant main effect of joint at each of the four fingers (index, p < 0.001; middle, p < 0.001; ring, p < 0.001; little, p < 0.001). Post-hoc tests revealed a larger ROM at the MCP joint compared with the PIP and DIP joints (p < 0.01 at all fingers). On average, the ROM at the MCP joint was larger than the PIP and DIP joint by 64.7% and 89.7%, respectively.

Rhythmic accuracy of keystrokes by the individual fingers

The group mean of the rhythmic error was computed for the VFB and NFB groups over the four practice days (Fig. 7). A non-parametric permutation test using group, practice session, and finger as independent variables yielded a significant two-way interaction between group and practice session (p = 0.001). The interaction effect confirmed a greater decrease in the error with practice for the VFB group than the NFB group, which indicates effectiveness of the present VFB for aiding in rhythmically accurate keystrokes.

DISCUSSION

In the present article, we investigated the effects of piano practice on individuated finger movements. A practice effect was evident, particularly at the MCP joint during the keystroke with the ring and little fingers, and it yielded more pronounced movement individuation. This finding provides evidence for the facilitation of



Fig. 4. The group mean and standard error of the correlation coefficients of the MCP joint motion between the middle and ring fingers during the ring finger strike (A), between the ring and little fingers during the ring finger strike (B), between the ring and little fingers strike (C), and the PIP joint motion between the ring and little fingers during the little finger strike (C), for the individuals in the NFB (red circle) and VFB (blue triangle) groups. The x-axis indicates the pre- and post-training sessions over 4 successive training days. An error bar indicates one standard error of the mean (SEM) across participants. A horizontal line in red and blue indicates a significant difference between sessions (p < 0.05) at each of NFB and VFB group, respectively. An asterisk in black indicates a significant group difference (p < 0.05). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

independent control of finger movements through piano practice. Although a number of studies have demonstrated reorganization of movements of the upper and lowerextremities through learning (Southard, 1989; Mason et al., 2001; Hodges et al., 2005; Yang and Scholz, 2005; Konczak et al., 2009), this study, to our best knowledge, is the first that characterized practice-related kinematic reorganization of the hand movements in terms of movement independence across fingers. A difficulty in moving fingers independently originates from the innate constraints of the hand, including the anatomical connection of tendons across fingers (Leijnse et al., 1993; Lang and Schieber, 2004a), the synchronized activity of motor units in different compartments of the multi-tendoned flexors and extensor of the digits (Kilbreath and Gandevia, 1994; Keen and Fuglevand, 2004; Winges et al., 2008), and the shared representation of individual fingers in the motor cortex (Schieber and Hibbard, 1993; Sanes et al., 1995). However, playing the piano requires moving fingers against these biomechanical and neurophysiological



Fig. 5. (A) Correlation coefficients of the MCP joint motion between all possible pairs of fingers during the strike with each of the four fingers at the pre-training session of the first day. The values were classified into two clusters according to whether there was a significant difference between sessions (right) or not (left). A threshold that distinguishes these two clusters is located at approximately 3.5 (a horizontal dotted line). The red and blue areas of the box plot indicate the 95% confidence interval and one standard deviation of each cluster, respectively. n.s.: non-significant (B) The relationship between the correlation coefficient at the pre-training session of the first day and the change in the coefficient value after the whole practice (i.e., day 4 post-training - day 1 pre-training) for the MCP ioint motion between all possible finger pairs during the strike with each of the four fingers in all participants. Each dot corresponds to one finger pair of one participant (3 finger pairs \times 4 fingers \times 10 participants = 120 points). A dotted line was drawn by the linear regression analysis. A negative regression indicates a larger decrease in the coefficient value at the finger pair with a higher coefficient value prior to the practice. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

constraints to perform a precisely timed sequence of movements with multiple fingers (Repp, 1995; Furuya et al., 2011a). Therefore, a lack of independent control of finger movements can result in an unwanted interaction between the fingers that are responsible for striking and lifting the keys, which may distort the rhythm, duration, and articulation of tone.

Repetition of the coupled movements between the finger flexion for striking and the extension for lifting under the strong temporal constraints during piano practice can elicit neuroplastic changes in the motor system (Kang et al., 2013). For example, compared with musically naïve individuals, musicians demonstrated reduced surround inhibition between muscles connected



Fig. 6. The group mean of the range of motion (ROM) at the MCP (black), PIP (gray), and DIP (white) joints of the index, middle, ring, and little fingers during the practice. The value was averaged across sessions and groups, due to a lack of their significant effects (see the main text). An error bar indicates one standard error of the mean (SEM) across participants. **p < 0.01; *p < 0.05.

to different fingers (Kang et al., 2012). Some studies have also reported a weaker synchronization of motor unit activity within a single hand muscle (Semmler and Nordstrom, 1998; Semmler et al., 2004) and a less pronounced difference in the cortical activity associated with the index and ring fingers for musicians compared with non-musicians (Slobounov et al., 2002). These neuroplastic adaptations may underlie the facilitation of the individuated finger movements through piano practice. The practice effect observed at the MCP joint, but not the PIP and DIP joints, may be attributed to a distinct difference in the amount of motion across the joints during the practice (Fig. 6).

Interestingly, only a few pairs of fingers specifically exhibited the practice effect, although all fingers were equally used in the current practice. Prior to the practice, the amount of movement independence was particularly low at these finger pairs (Fig. 5A), which indicates that the practice effect was limited to the fingers with intrinsically low independent control. This idea was further supported by the results of the regression analysis, which demonstrated a larger improvement in independence at the finger with lower independence (Fig. 5B). These findings imply a difference in neuromuscular plasticity across fingers. Previous studies have demonstrated equal independence of movements across fingers for expert pianists (Furuya et al., 2011a), but not for musically



Fig. 7. The group mean and standard error of the rhythmic error of keystrokes with each of the index (A), middle (B), ring (C), and little (D) fingers for the individuals in the NFB (red circle) and VFB (blue triangle) groups. The *x*-axis indicates the pre- and post-training sessions over 4 successive training days. An error bar indicates one standard error of the mean (SEM) across participants. A horizontal line in red and blue indicates a significant difference between sessions (p < 0.05) at each of NFB and VFB group, respectively. An asterisk in black indicates a significant group difference (p < 0.05). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

untrained individuals (Häger-Ross and Schieber, 2000; Zatsiorsky et al., 2000), which also suggests a different capacity of training across fingers.

Overall, the correlation coefficient values were relatively closer to zero for the VFB group compared to the NFB group (Fig. 4). In addition, a clear group difference was present for the movement independence between the ring and little fingers during the little finger keystroke at both MCP and PIP joints. This finding suggests that VFB has beneficial effects on enhancing the independent control of finger movements, which corroborates with previous findings of facilitation of motor skill acquisition by augmented feedback (Debaere et al., 2003; Ronsse et al., 2011; Sigrist et al., 2013). Precise information on movement accuracy may serve as an error signal to correct motor commands and update internal representation of the hand neuromuscular system via supervised learning (Kawato, 1999). The explicit provision of error-related information can be of particular help for untrained individuals whose perceptual abilities are not well-developed (Herholz and Zatorre, 2012). The enhancing effect can also be associated with an increased neuroplasticity of the motor system by visual attention (Stefan et al., 2004).

A question arises to which extent the current practice effects transfer to untrained motor tasks. Our recent study demonstrated that 4-days of piano practice at a submaximal tempo enhanced the maximum speed of finger movements not only at the trained sequence but also the untrained sequence (Furuya et al., 2013). However, the maximum speed of repetitive finger tapping while immobilizing the remaining digits did not increase. In combination with the present finding, effects of practice on independent control of finger movements may generalize to tasks similar to the practice motor task, and to irrelevant tasks only through practicing for longer period and/ or in wider contexts of movements.

The current study may have potential implications for the use of piano practice to enhance the hand dexterity of elderly individuals and patients with movement disorders. The independent control of finger movements plays a crucial role in the dexterous use of tools and hands. A loss of this motor function through aging (Shim et al., 2004) and movement disorders such as stroke (Lang and Schieber, 2004b; Raghavan et al., 2006), cerebellar damage (Brandauer et al., 2012), and Parkinson's disease (Park et al., 2012) severely degrades the quality of life. Playing the piano has several advantages over conventional physical therapies such as a constraintinduced movement therapy; these advantages include the auditory feedback of the motor actions (Furuya and Soechting, 2010) and the emotion and reward evoked by a musical performance (de Manzano et al., 2010; Nakahara et al., 2011). These enriched sensory and cognitive experiences may serve as ingredients driving neuroplastic adaptations in the motor system and thereby facilitate fine motor control (Rodriguez-Fornells et al., 2012; Grau-Sanchez et al., 2013). However, the current study cannot rule out alternative explanations such as a shift in attentional focus across the practice sessions to the goal of the action rather than the movements involved in producing the goal.

Several limitations of the present study should be improved in future studies, such as a limited number of participants, lack of neurophysiological evaluation of the practice effect, and evaluation of differences in transfer and retention effects between groups. In particular, it should be evaluated whether the results would change with a larger sample size. Another interesting issue is a comparison of practice effects across different perceptual modalities used for feedback presentation (Ronsse et al., 2011).

In sum, the present study demonstrated enhancement of the individuated finger movements after daily piano practice. The learning gain was larger at the finger pairs with potentially low independent movement control. Provision of extrinsic VFB regarding rhythmic error of keystrokes facilitated the practice effect selectively for a subset of finger pairs. The results highlight the potential of piano practice for improving the dexterous use of the hand, which is of particular importance for elderly individuals and patients with movement disorders causing loss of hand dexterity.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

CONTRIBUTIONS

Conceived and designed the experiments: SF, Performed the experiments: AN, Analyzed the data: SF AN, Wrote the paper: SF AN NN.

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