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EXPERTISE-DEPENDENT MODULATION OF MUSCULAR AND NON-MUSCULAR TORQUES IN MULTI-JOINT ARM MOVEMENTS DURING PIANO KEYSTROKE

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Abstract—The problem of skill-level-dependent modulation in the joint dynamics of multi-joint arm movements is addressed in this study using piano keystroke performed by expert and novice piano players. Using the measured kinematic and key-force data, the time varying net, gravitational, motion-dependent interaction (INT), key-reaction (REA), and muscular (MUS) torques at the shoulder, elbow, wrist, and metacarpophalangeal (MP) joints were computed using inverse dynamics techniques. INTs generated at the elbow and wrist joints, but not those at the MP joint, were greater for the experts as compared with the novices. REA at the MP joint, but not at the other joints, was less for the experts as compared with the novices. The MUSs at the MP, wrist, and elbow joints were smaller, and that at the shoulder joint was larger for the experts as compared with the novices. The experts also had a lesser inter-strike variability of key striking force and key descending velocity as compared with the novices. These findings indicated that the relationship among the INT, REA, and MUS occurring at the joints of the upper-extremity differed between the expert and novice piano players, suggesting that the organization of multi-joint arm movement is modulated by long-term motor training toward facilitating both physiological efficiency and movement accuracy.

Key words: motor control, multi-joint movement, expertise, non-muscular force, pianist.

When moving limbs with multiple joints, the CNS must coordinate the muscular forces with both the externally applied forces and the internally arising forces associated with the movement itself. In common upper limb movements, the external forces include gravity (GRA) and reaction forces arising from the manipulated objects, while the internal forces include the interaction forces that act on a limb segment because of the motion of the adjacent segments. The rotational effects of these forces at the joints of the moving limb and the corresponding torques arising from the muscles (MUS) that commonly include passive anatomical properties, GRA, mechanical interaction with the external environment (REA), and inter-segmental interaction (INT) are estimated from a kinetic analysis of a moving limb (Dounskaia et al., 2002; Gribble and Ostry, 1999; Goble et al., 2007; Hirashima et al., 2003a, 2007; Putnam, 1993; Shadmehr and Mussa-Ivaldi, 1994). The findings from these studies suggest that successful multi-joint movements require effective feedforward exploitation and/or compensation of INTs, which can be learned by training. Using rapid sagittal target-reaching and reversal arm movements over an obstacle, Schneider et al. (1989) examined the effects of training on the performance and torques arising at the shoulder, elbow, and wrist joints. They found that the performance after 100 trials in less than 1 h was characterized by a shortened movement duration, and this was accompanied by an increase in MUS and INT at all joints involved in the movement. Marconi and Almeida (in press) recently used horizontal target-reaching and reversal shoulder-elbow movements and tested the effect of 1 day of training on the performance and torques at the shoulder and elbow joints. Similar to the findings of Schneider et al. (1989), Marconi and Almeida found that with training, the peak velocity increased and thus the movement time decreased. The elbow extension INT increased significantly while neither the associated MUS nor elbow flexor and extensor muscular activities changed after training. These two studies have therefore shown that an improvement in the performance in terms of speeding up the limb movements can occur because the subjects have learned the use of greater magnitudes of INTs with training. On the other hand, an improvement in the performance in terms of physiological and mechanical efficiency, and thus a decrease in the MUS, may be another important issue related to the effect of training on inter-segmental dynamics. Indirect evidence of this has been reported by Sainburg and Kalakanis (2000), who compared the inter-segmental dynamics of dominant and nondominant arms during a constant speed target-reaching task. They found a smaller elbow extension MUS with a larger INT in the dominant side as compared with the nondominant side. These findings suggested that with years of training, the CNS could maximize the use of INTs and minimize the muscular work to a complementary level for performing the task, supporting the idea of Bernstein (1967). A problem with the dominant–nondominant comparison is that in addition to a clear skill level difference due to both the quality and quantity of daily use, the differential effects of genetic contributions to the hemispheric asymmetries of the neural circuit for the control of arm movements cannot be excluded (Serrien et al., 2006;

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Abbreviations: CV, coefficient of variation; DIP, distal–interphalangeal; DOF, degree of freedom; GRA, gravitational torque; INT, inter-segmental interaction torque; MP, metacarpophalangeal; MUS, muscular torque; NET, sum of all the torques acting at a joint; PCSA, physiological cross-sectional area; PIP, proximal–interphalangeal; REA, key-reaction force torque; SPL, sound pressure level.

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Tan and Tan, 1999). Consequently, there has been no direct evidence of a skill-level-dependent decrease in MUSs via the increased exploitation of INTs. A solution for this may be the selection of a task that requires constant movement speed, and subjects with different skill levels.

Piano keystroke may be a motor task suitable to approach this problem (Furuya and Kinoshita, 2007, 2008). These motions commonly begin with the lifting of the entire arm to some height, dropping it for the finger(s) to hit and depress the target key(s) against the reaction force from the key with a velocity determined by the target loudness level of the eliciting tone, and lifting the hand again to release the key depression. A comparative study of keystroke by expert and novice piano players can therefore provide a unique opportunity to investigate the effect of long-term training on the joint dynamics of a complex, but natural multi-joint motor action. In our recent studies of upper limb kinematics in expert and novice piano players who performed a similar keystroke motion, we found that the experts had a larger maximum deceleration of the descending motion at the upper-arm and forearm but not at the hand as compared with the novices (Furuya and Kinoshita, 2007, 2008). We thus hypothesized that a training-related reduction in the MUSs would occur by effectively exploiting the INTs generated at the elbow and wrist joints, but not at the metacarpophalangeal (MP) joint. The primary purpose of the present study was to test this hypothesis by applying an inverse dynamic analysis on a four-linked upper limb segment model to the kinematic data obtained from the keystroke of expert and novice piano players. A direct measurement of the key-depressing force was also performed during the keystroke to permit the analysis of inter-segmental dynamics during the key depression phase. This can further permit an investigation of the effect of long-term training on the compensation of external reactive forces that would produce perturbing joint torques (REA). Previous studies have reported no training-related reduction in the REA (Burdet et al., 2001; Franklin et al., 2003). The findings from our earlier kinematic study of key depression, on the other hand, suggested that the expert pianists might have smaller REAs at the MP joint as compared with the novices (Furuya and Kinoshita, 2008). This was because the experts depressed the key with a higher angle of attack of the fingers as compared with the novices so that the MP joint center was located closer to the finger-key contact point. This allows the experts to have a shorter moment arm for the torque generated at the MP joint, but not for the other joints. The secondary purpose of this study was therefore to investigate the difference between experts and novices in terms of the REAs and compensating MUSs at the upper limb joints.

EXPERIMENTAL PROCEDURES

Participants

Seven active expert pianists (three males and four females, mean age±S.D.=24.3±3.2 years) with more than 15 years of classical piano training, and seven novice piano players (three males and four females, age=21.0±4.6 years) with less than a year of piano training participated in the present study. All the expert pianists had won awards at domestic and/or international classical piano competitions. In order to exclude the possibility that any differences in the keystroke motions across pianists were attributed to the technique that had been intensively taught at a certain piano school, participants who had learned to play the piano from different instructors were selected. All participants were right-handed, as determined by the Edinburgh MRC Handedness Inventory (Oldfield, 1971). Informed consent was obtained from all participants, and the study was approved by the ethics committee at Osaka University.

Experimental apparatus and key-striking task

The experimental apparatuses used were a Yamaha U1 upright piano, two 2-D position sensor systems (C5949, Hamamatsu Photonics Co., Japan), a sound-level meter (NA-27, Rion Co., Japan), and a stereo sound amplifier. In the G3-key, a strain-gauge miniature uniaxial force transducer was installed at its distal end (see details in Kinoshita et al., 2007). The resolution of the transducer was 0.02 N, and the natural frequency of the unloaded force transducer was DC 1 kHz. The force signal was amplified using a strain gauge amplifier (DMP602B, Kyowa Co., Japan). The sound-level meter was placed 1 m above the keyboard. All signals from the position sensor, the amplifier of the force transducer, and the sound-level meter were stored on a Sony personal computer via a 12-bit A/D converter with a sampling frequency of 900 Hz.

The experimental task was a right-hand octave keystroke, a simultaneous strike of the 35th (G3) key by the thumb and the 47th (G4) key by the little finger. These keys were 166 mm apart. This movement task was selected to induce a whole arm movement, as well as to minimize the medio-lateral and pronation-supination movements of the hand and arm during the keystroke so as to restrict the upper-limb movements within the sagittal plane in accordance with the motion analysis used by the present authors (see Data acquisition procedure). We had previously assessed the magnitude of the medio-lateral as well as pronation-supination movements using a 3-D kinematic analysis, and found that it was sufficiently small to warrant the validity of the 2-D analysis method (Furuya et al., 2006a).

In the experiment, a participant began with the fingertips of the right hand lightly touching the keys, lifted his/her right arm/hand to a self-determined height at a self-determined speed, and stroked the keys in a short tone production (a staccato touch) at a designated level of tone. The participant then lifted his/her hand and arm again as a follow-through to a self-determined height, and returned to the initial position. The left arm and hand were kept relaxed and placed on the side of the trunk while the trunk was in an upright position with minimal movement.

Four target sound pressure levels (SPLs) of 103, 106.5, 110, and 113.5 dB were selected in this study, which roughly corresponded to the loudness levels for a piano (*p*), mezzo-piano (*mp*), mezzo-forte (*mf*), and forte (*f*), respectively (Furuya and Kinoshita, 2007, 2008; Kinoshita et al., 2007). Kinematic and simultaneous sound data were collected from 30 successful strokes at each target SPL with a trial-to-trial interval of approximately 10 s for each participant. The target SPL was a prerecorded piano sound on a minidisk, which was presented from a set of speakers placed on top of the piano. With the help of the experimenter providing feedback regarding the difference in the produced and given SPLs, each participant practiced the task until he/she could reduce the errors to within ±0.9 dB of the target SPL before the data collection. This practice session was provided to each participant for maximally 5 min. During the data collection, a trial with a tone above or below 0.9 dB of the target SPL was asked for a retrial.

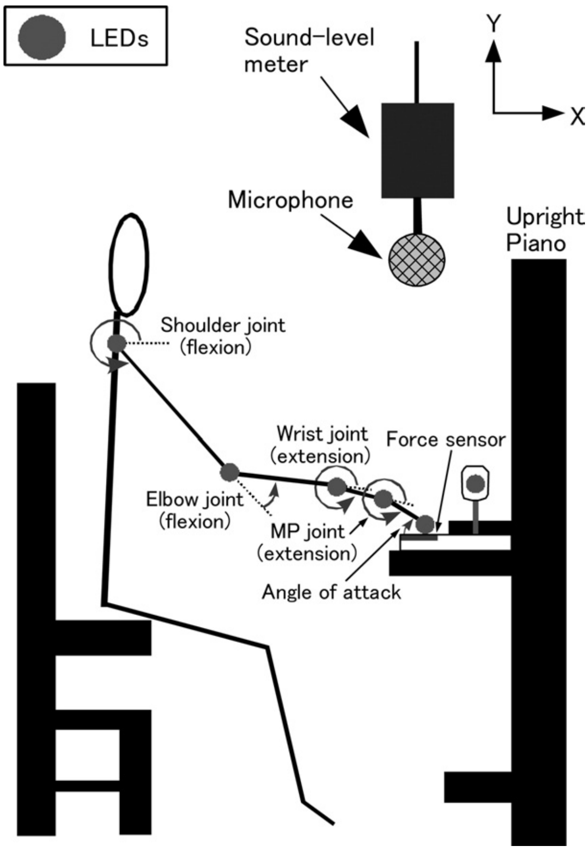

Fig. 1. LED placement and definition of joint angles. The counterclockwise direction is defined as a positive direction for the angular displacement at each joint. A positive angular displacement describes the flexion movement at the shoulder and elbow joints and the extension movement at the wrist and MP joints.

Data acquisition procedure

The movement of the upper limb in the sagittal plane was recorded using one of the position sensor cameras (sampling freq.=150 Hz) located 3.5 m to the right of the participant. The LEDs required for this purpose were mounted on the skin over the fingertip of the little finger and at the centers of the MP (finger), styloid process (wrist), head of radius (elbow), and coracoid process (shoulder) joints (Fig. 1). In order to minimize the measurement errors, the rotational center of each joint was carefully estimated. For this purpose, we always recorded the joint movement after attaching the LEDs on the skin on video to visually check if each LED was positioned at the center of rotation of the target joint. The data were digitally smoothed at a cutoff frequency of 10 Hz using a second-order Butterworth digital filter. The angular displacement at the MP, wrist, elbow, and shoulder joints, and that of the little finger segment relative to the key surface were then numerically calculated (see definition of the joint angles in Fig. 1). Because there was no position data at the proximal–interphalangeal (PIP) and distal–interphalangeal (DIP) joint centers in the present experiment, we approximated the MP joint angle as the angle formed by the vectors from the MP joint center to the fingertip of the little finger and from the MP joint center to the wrist joint center. The participants were requested to maintain a similar finger posture (the PIP and DIP joints) across all dynamics tested. None of all participants reported that this instruction prevented from performing their natural keystroke motion.

From the computed joint angle data, several discrete kinematic variables were computed. These included the angle of the finger segment relative to the key (=angle of attack) at the moment of the key's maximum displacement, and movement amplitudes of the rotation of the finger segment, and the rotations of the MP, wrist, elbow, and shoulder joints during the key-depression period (between the moment of finger-key contact and the moment of the key's lowest position).

Key kinematics and kinetics

The G3-key kinematics was recorded using another position sensor camera located 0.65 m to the left of the key and an LED placed on the key surface. The key position data were numerically differentiated to obtain its velocity data. The peak key's descending velocity was then determined. The onset of the key descending movement ("the finger-key contact moment") was determined when the calculated vertical velocity of the key exceeded 5% of its peak. The movement of the G4 key was not measured due to the difficulty involved in placing a close-up camera to the right of the piano without interfering with the kinematic recording of the hand movement by the far camera. In our previous study, a high spatiotemporal synchrony of the G3 and G4 keys during keystroke similar to that in the present study was confirmed for both experts and novices (Furuya and Kinoshita, 2007).

In order to determine if the inter-strike variability of the key-striking motion differs between the experts and novices, the coefficient of variation (CV) of the peak key-descending velocity and peak key-reaction force for 30 strikes was evaluated at each loudness level (Table 1). The CV value was computed by dividing the standard deviation of each variable by the mean value.

Inverse dynamics computation

Using the measured kinematic and key-force data along with the anthropometric data of each participant, the inverse dynamics equations were used to calculate the time varying net (NET), GRA, motion-dependent INT, key-reaction force (REA), and MUS torques at the shoulder, elbow, wrist, and MP joints (see Appendix for details). For the purpose of this study, the upper extremity was assumed as four interconnected rigid links (upper arm, forearm, hand, and finger). The fingers that remained unused for key-striking were also assumed to be fixed to the hand, and their inertia properties were included in the hand segment (Dennerlein et al., 2007). The measured data and body segment parameters for a Japanese individual were used for the upper arm, forearm, and hand segments (Ae et al., 1992). The finger segment was approximated by uniform cylindrical tubes with ellipsoid cross-sections, and their masses and the moments of inertia were estimated using the density of water (Dennerlein et al., 1998; Kuo et al., 2006). The effect of trunk movement on these kinetic computations was not considered because it was nearly negligible (horizontal and vertical movements of the shoulder joint center were all less than 6 mm and 7 mm in all participants, respectively). NET was defined as the sum of all the torques acting at a joint, which was estimated by taking the product of the moment of inertia of the involved segments and the angular acceleration around a given joint. GRA was the torque produced by the gravitational force acting on the limb segments of the arm. This torque changes in relation to the limb posture. INT mechanically arises because of the motion of the linked segments. In the present study, INT was determined as the sum of centripetal, coriolis, and inertial torques (Bastian et al., 1996; Hirashima et al., 2003a), and its magnitude varied with the velocity and acceleration of the joint movements in the linked segments. REA was the torque arising from the key reaction force, and its magnitude varied with both the magnitude of the key force and the limb posture (Furuya and Kinoshita, 2008). MUS was calculated by subtracting the sum of the computed INT, GRA, and REA from the NET. Accordingly, the

Table 1. Mean and CV values of key reaction force and key-descending velocity

Variables	Experts				Novices				ANOVA results (*F* value)		
	p	*mp*	*mf*	*f*	*p*	*mp*	*mf*	*f*	Group	Loudness	Group×loudness
Peak key reaction force (N)	4.9 (1.2)	8.3 (1.1)	16.1 (1.6)	23.7 (3.1)	4.8 (1.5)	7.2 (1.7)	12.4 (2.0)	20.2 (5.5)	4.4	189.4***	2.6
Peak key velocity (mm/s)	121.8 (15.7)	160.2 (15.5)	195.6 (19.0)	217.4 (15.2)	116.7 (14.5)	155.0 (10.6)	186.2 (9.0)	210.9 (10.8)	0.9	423.6***	0.2
CV of peak key reaction force (%)	11.5 (2.4)	11.8 (1.2)	11.2 (2.2)	10.4 (1.5)	16.3 (3.5)	16.0 (3.7)	15.2 (2.9)	17.1 (4.5)	12.9**	0.5	1.8
CV of peak key velocity (%)	7.4 (1.7)	6.0 (2.1)	4.0 (1.5)	3.5 (1.1)	12.5 (1.9)	10.0 (3.0)	6.1 (2.7)	5.6 (1.7)	12.0**	70.4***	5.7**

The numbers in the parentheses indicate the standard deviation.
** $P<0.01$.
*** $P<0.001$.

MUS did not represent the "pure" muscular torque generated only by muscular contraction. The passive torques arising from the muscles, tendons, ligaments, articular capsules, and other connective tissues were also included.

MUS can be separated into static and dynamic components (Gottlieb et al., 1996; Guigon et al., 2007). The former counteracts the effect of GRA to maintain the limb posture; thus, it can have a magnitude equivalent to GRA but acting in the opposite direction. The latter, on the other hand, is used for the limb movements; it is the residual MUS after subtracting GRA (MUS−|GRA|). Although Gottlieb et al. (1996) used a constant GRA value for simplicity in the computation of MUS−|GRA|, we used a GRA that varied depending on the limb angular position. In the present study, MUS−|GRA| was referred to as "MUS^+" for simplicity.

In order to quantify the amount of MUS^+ and INT that assist in the descending motion of the finger, and the REA produced during the key-depression, we calculated the impulses of the MUS^+, INT, and REA at the shoulder, elbow, wrist, and MP joints as follows:

$$MUS\mathrm{Im}=\int_{T1}^{T2} M(t)\,dt$$

$$INT\mathrm{Im}=\int_{T1}^{T2} I(t)\,dt$$

$$REA\mathrm{Im}=\int_{T1}^{T2} R(t)\,dt$$

$$NET\mathrm{Im}=\int_{T1}^{T2} N(t)\,dt$$

where T1 is the time of movement onset (the highest hand position) and T2 is the time of the lowest key position, when the key-depression was ended, and $M(t)$ and $I(t)$ are the time-varying MUS^+ and INT, respectively. $R(t)$ is the time-varying REA that occurs during key depression. These were calculated as follows:

$$M(t)=\begin{cases} MUS^+(t) & (MUS^+(t)>0{:}\,shoulder;\ MUS^+(t)<0{:}\,elbow, wrist, MP) \\ 0 & (MUS^+(t)<0{:}\,shoulder;\ MUS^+(t)>0{:}\,elbow, wrist, MP) \end{cases}$$

$$I(t)=\begin{cases} INT(t) & (INT(t)>0{:}\,shoulder;\ INT(t)<0{:}\,elbow, wrist, MP) \\ 0 & (INT(t)<0{:}\,shoulder;\ INT(t)>0{:}\,elbow, wrist, MP) \end{cases}$$

$$R(t)=REA(t)\ \ (REA(t)>0{:}\,shoulder, elbow,\ wrist,\ MP)$$

$$N(t)=\begin{cases} NET(t) & (NET(t)>0{:}\,shoulder;\ NET(t)<0{:}\,elbow, wrist, MP) \\ 0 & (NET(t)<0{:}\,shoulder;\ NET(t)>0{:}\,elbow, wrist, MP) \end{cases}$$

In this analysis, MUS^+, INT, and NET for shoulder flexion, elbow extension, wrist flexion, and MP flexion were integrated to assess contribution of the joint torques to the production of descending motion of the finger during the entire keystroke period. Accordingly, the joint torques contributing to lifting the finger upward were set as zero in this analysis.

Additional test of endurance for repetitive piano keystrokes

In order to determine if the keystroke motion of the experts was more efficient by a greater use of INTs and reduction in REAs with a greater reduction in muscular work, an additional test of prolonged repetitive keystrokes was conducted using four experts and four novices from the present participants. The participants were asked to perform a right-hand octave keystroke for as long as possible at a striking tempo of 4 Hz while maintaining the predetermined forte dynamics (SPL>111.5 dB). The experiment for the endurance test was terminated either after 30 min passed from the beginning of this experiment or when the performers could not continue to produce the target SPL for more than 2 min. The duration of this experiment was considered as a measure of the endurance against muscular fatigue from the keystroke.

Statistical data analysis

Using group (a between factor) and loudness (a within factor) as independent variables, a two-way ANOVA with repeated measures was performed for each of the dependent variables. The statistical significance was set at $P<0.05$.

RESULTS

Expert–novice difference in torque profiles

The representative mean time-history curves of NET, MUS$^+$, INT, and REA at the shoulder, elbow, wrist, and MP joints at the forte dynamics in one expert and one novice are shown in Fig. 2. The torque profiles in the other players for each of the expert and novice groups were quite similar to these examples.

Shoulder joint. During the arm-descending period, relatively large shoulder NET, MUS$^+$, and INT were observed for the expert; however, this was not the case in the novice (the shoulder, shown in Fig. 2). The relationship among these torques indicated that the increase in NET for the expert was accompanied by an increase in MUS$^+$. This MUS$^+$ increase corresponded with a decrease in its extension MUS$^+$ initially, followed by an increase in the flexion MUS$^+$. This increase in the flexion muscular torque clearly differentiated the expert's keystroke from that of the novice. The flexion and extension INTs developed at the shoulder joint also contributed to the increase in shoulder NET for the expert. For the novice, a shoulder flexion INT was also developed with the descending of the arm. The resulting NET was, however, quite small due to the presence of a counteractive extension MUS$^+$. During the key depression, a large flexion REA was developed at the shoulder joint; this REA was nearly equal for both the expert and novice. This REA was counteracted with the extension INT for the expert, and a combination of extension INT and MUS$^+$ for the novice.

Elbow joint. During the arm-descending period, a clear elbow extension NET was observed in both the expert and novice (elbow in Fig. 2). An expert–novice difference was however found for INT and MUS$^+$. For the expert, a large extension INT was developed from the middle of the arm descent to the end of the key depression phase. This INT was counteracted by the increased flexion MUS$^+$ and REA. For the novice, on the other hand, the INT produced was quite small during the arm descent, and there was almost no counteractive flexion MUS$^+$. In addition, the novice had a large extension MUS$^+$ during the key depression phase.

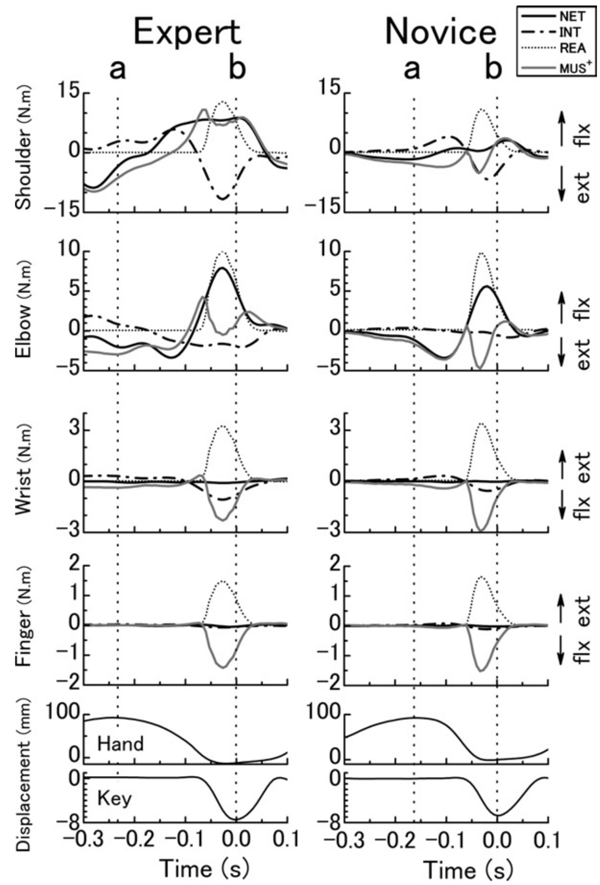

Fig. 2. The time-history curves of the computed NET (solid line), INT (dashed line), REA (dotted line), and MUS$^+$ (gray line) at the shoulder, elbow, wrist, and MP joints, and key and hand vertical position at the forte loudness level, for one representative expert (left panel) and novice (right panel) piano player. The curves represent the average of 30 keystrokes. The dotted vertical lines indicate the moment of the highest hand position (a) and the lowest key position when the key-depression was ended (b).

Wrist joint. The torque produced at the wrist joint was smaller than those at the shoulder and elbow joints. For both the expert and novice, the extension INT generated prior to the onset of downswing ("a" in Fig. 2) gradually decreased as the arm descended, which reversed into flexion torque prior to the finger-key contact moment. The flexion INT then increased markedly to reach a peak just before the key bottom moment ("b" in Fig. 2). This strong flexion INT results from a combination of increased flexion NET at the elbow and shoulder joints. The expert had a relatively larger flexion INT and smaller flexion MUS$^+$ as compared with the novice. The wrist flexion MUS$^+$ also increased largely to counteract the increased extension REA. Consequently, the NET produced at the wrist remained close to zero throughout the keystroke.

MP joint. The MP-joint torques were all close to zero during the descending period for both the expert and novice. During key depression, a large extension REA and flexion MUS$^+$ evolved in both sets of players. This resulted in a small and constant NET. The flexion INT was also

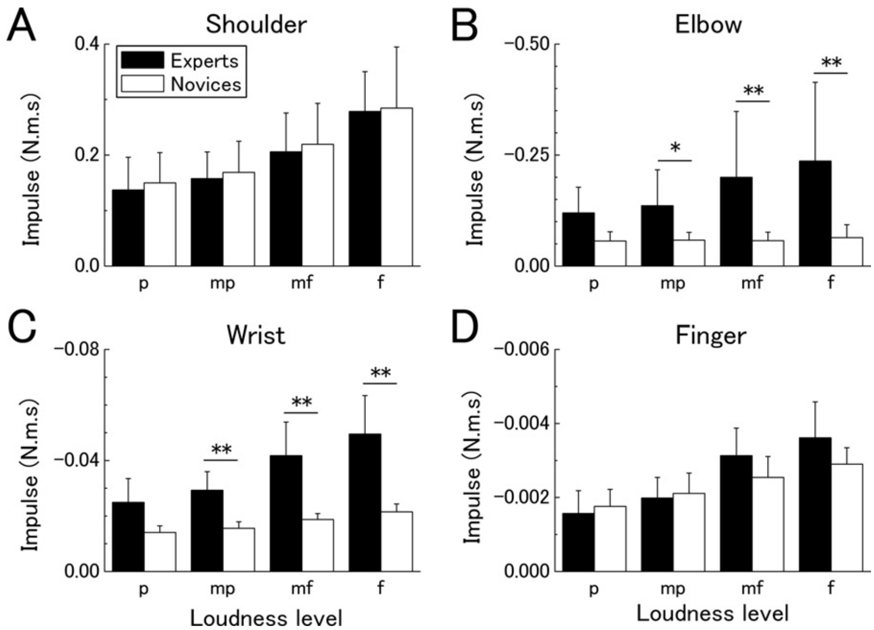

Fig. 3. The group means of the INTIm for shoulder flexion (A), elbow extension (B), wrist flexion (C), and MP flexion (D) during a keystroke. * $P<0.05$, ** $P<0.01$. The error bars represent ± 1 S.D.

observed during this period; however, its magnitude was much smaller as compared with the MUS^{+} and REA.

Expert–novice difference in torque impulse

A statistical comparison between experts and novices was made using the torque impulse values.

Interaction torque. Fig. 3A–D shows the group means of the INTIm at each loudness level. ANOVA revealed that the experts had a significantly larger INTIm for elbow extension ($F(1, 12)=7.04$, $P=0.021$) and wrist flexion ($F(1, 12)=33.75$, $P<0.001$) than the novices. The group×loudness interaction was also significant in this variable for the elbow extension ($F(3, 36)=4.20$, $P=0.012$) and wrist flexion ($F(3, 36)=7.28$, $P<0.001$). The interaction effect indicated that with the generation of louder sound, the experts produced larger elbow extension and wrist flexion INTIm than the novices. The loudness effect was significant at all joints ($P<0.01$).

Muscular torque. Fig. 4A–D shows the group means of the *MUS*Im at each loudness level. ANOVA revealed a significantly smaller *MUS*Im for elbow extension ($F(1, 12)=24.67$, $P<0.001$), wrist flexion ($F(1, 12)=27.73$, $P<0.001$), and MP flexion ($F(1, 12)=16.55$, $P=0.002$), and a larger MUSIm for shoulder flexion ($F(1, 12)=12.97$, $P=0.004$) for the experts as compared with the novices. The group×loudness interaction was also significant for the shoulder flexion ($F(3, 36)=4.56$, $P=0.008$) and elbow extension ($F(3, 36)=4.77$, $P=0.007$), and it was close to the level of significance for wrist flexion ($F(3, 36)=2.42$, $P=0.08$). The interaction effect indicated that the group difference in these joint torques was larger for the production of louder sound. The loudness effect was significant at all joints ($P<0.05$).

Key force torque. Fig. 5A–D shows the group means of the *REA*Im at each loudness level. ANOVA revealed a smaller *REA*Im for MP extension ($F(1, 12)=38.18$, $P<0.001$) for the experts as compared with the novices. There was no group×loudness interaction at all joints. The loudness effect was significant at all joints ($P<0.001$).

Net torque. Fig. 6A–D shows the group means of the NETIm at each loudness level. ANOVA revealed that the experts had a significantly larger NETIm for shoulder flexion ($F(1, 12)=9.45$, $P<0.001$) as compared with the novices. The group×loudness interaction was also significant for the shoulder flexion ($F(3, 36)=4.99$, $P=0.005$), indicating a larger group difference for the louder sound production. The loudness effect was significant at all joints ($P<0.05$).

Key reaction force, key descending velocity, and angle of attack

Table 1 lists the group means and CVs of the peak key reaction force and peak key descending velocity at each loudness level, and the results of ANOVA. There was a significant loudness effect for the means of these variables. Neither the group main effect nor the effect of the interaction between the group and loudness was significant. For the CV of peak key reaction force, the experts had a smaller value as compared with the novices. For the CV of peak key descending velocity, the effects of group×loudness interaction, group, and loudness were all significant (Table 1). The interaction effect indicated that with the generation of louder sound, the novices had a greater decrease in velocity CV as compared with the experts. The experts also had a smaller CV as compared with the novices.

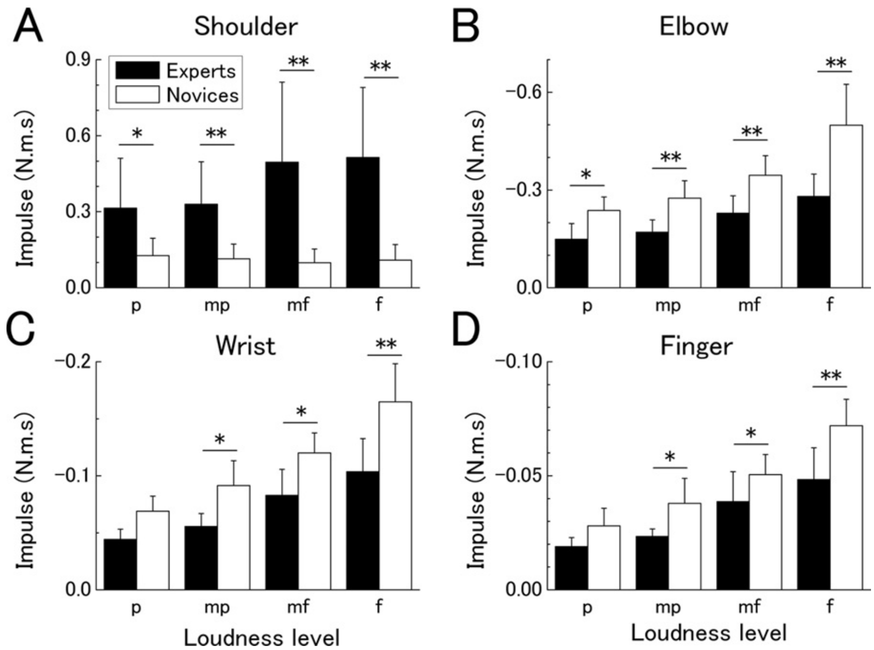

Fig. 4. The group means of the MUSIm for shoulder flexion (A), elbow extension (B), wrist flexion (C), and MP flexion (D) during a keystroke. * $P<0.05$, ** $P<0.01$. The error bars represent ±1 S.D.

The mean angles of attack at the moment of key bottom for all participants were significantly larger for the experts as compared with the novices at all SPLs ($F(1, 12)=69.26$, $P<0.001$, Fig. 7A). The ranges of their angular rotation during the key depression phase were also significantly larger for the experts than the novices ($F(1, 12)=8.08$, $P=0.015$, Fig. 7B).

In order to examine how the experts achieved such a large increase in the angle of attack during key depression, a multiple-regression analysis was performed using the movement amplitude of their MP flexion and extension, wrist flexion, elbow extension, and shoulder extension and flexion as independent variables. An R^2 value of 0.82 was obtained in this analysis. The highest contribution to this was the shoulder flexion (semi-partial correlation=0.33), followed by the finger flexion (0.25), and wrist flexion (0.21). The contribution of all others was less than 0.12. These results confirmed our previous finding that the ex-

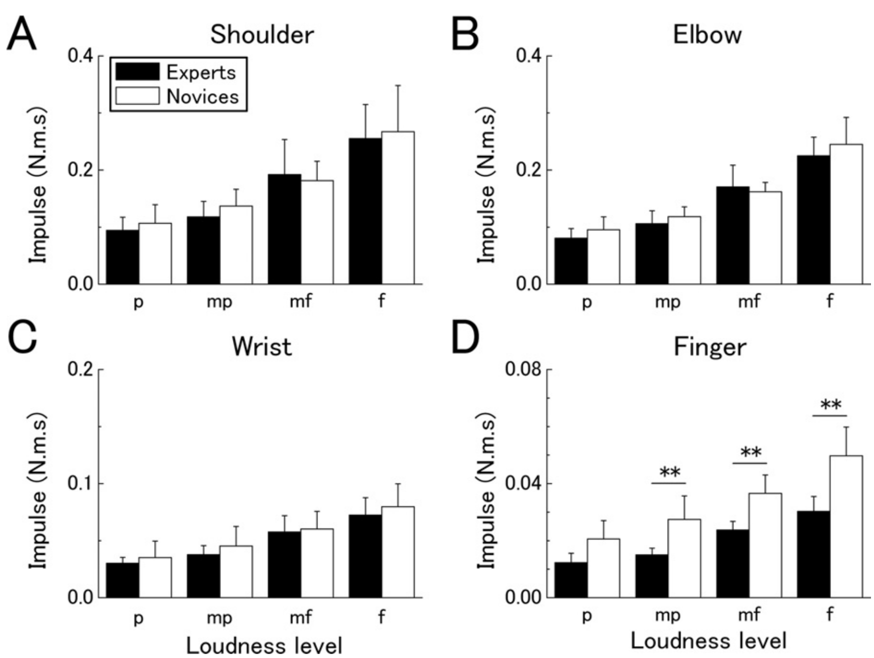

Fig. 5. The group means of the REAIm for shoulder flexion (A), elbow flexion (B), wrist extension (C), and MP extension (D) during a keystroke. * $P<0.05$, ** $P<0.01$. The error bars represent ±1 S.D.

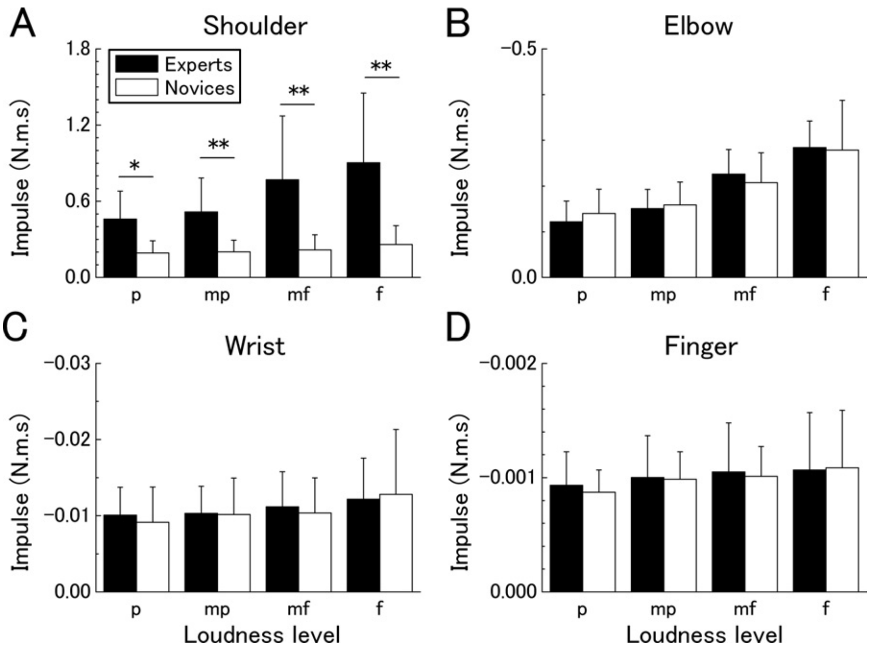

Fig. 6. The group means of the NETIm for shoulder flexion (A), elbow extension (B), wrist flexion (C), and MP flexion (D) during a keystroke. * $P<0.05$, ** $P<0.01$. The error bars represent ±1 S.D.

perts produced a vigorous shoulder flexion motion during key depression, and thereby achieved a larger angle of attack as compared with the novices (Furuya and Kinoshita, 2008).

Endurance test results

The effect of repetitive keystrokes on the produced SPL for each of the eight participants is shown in Fig. 8. All four experts did not exhibit any decline in the SPL until the end of 30 min. On the other hand, all the novices began to exhibit a clear decrease in the SPL after 5 min. Three of the novices failed to continue the target SPL production for 10 min, and one novice failed by 15 min. Clearly, the experts demonstrated the ability of greater keystroke endurance as compared with the novices.

DISCUSSION

We compared inter-segmental dynamics of upper limb movements when striking the piano keys between expert and novice piano players. Although some previous researchers have considered the effect of learning on control of multi-joint movements, laboratory tasks and short-term practice sessions were commonly used. The present study first time presented the effect of long-term learning on a natural movement, providing unique demonstration of the principles used by the CNS to adapt and develop highly skillful arm movements.

Skill level difference in MUS and interaction torques

Bernstein (1967) had previously proposed that with an improvement in motor skills, the motor system would take greater advantage of passive forces such as reactive and inertial forces to make movements more economical. The present study clearly demonstrated that for the downward arm swing motion including depression of the keys by the experts, the muscular work estimated from the MUSs at the elbow and wrist joints was indeed significantly less while the inertial, centripetal, and coriolis forces estimated from the INTs at the corresponding joints were significantly larger as compared with those of novices. We also confirmed that the values of NETs and REAs at these joints were similar between the two groups, indicating that larger MUSs and smaller INTs for the experts occurred in a reciprocal manner. This, however, was not the case in some of the previous studies that examined the effect of practice on inter-segmental dynamics of the arm for reaching a target without the control of movement speed. Schneider et al. (1989) have shown that both MUSs and INTs are increased along with an increase in the movement speed after repeating the same task 100 times, and Marconi and Almeida (in press) have shown only INTs are increased with an increase in movement speed after practicing the task for 1 day. With the control of movement speed and using groups of subjects having a clear difference in training period, we confirmed that the exploitation of INTs at the distal joints became strong enough for the experts to reduce the muscular work associated with distal segmental motion, which clearly supported the hypothesis of Bernstein (1967).

Dounskaia (2005) recently proposed that the CNS organizes multi-joint movements by using a hierarchical control as follows. There is one (leading) joint that generates powerful INTs at the other (subordinate) joints. The INTs are then exploited to assist the generation of motion at the subordinate joints. The proximal joint tends to be a leading

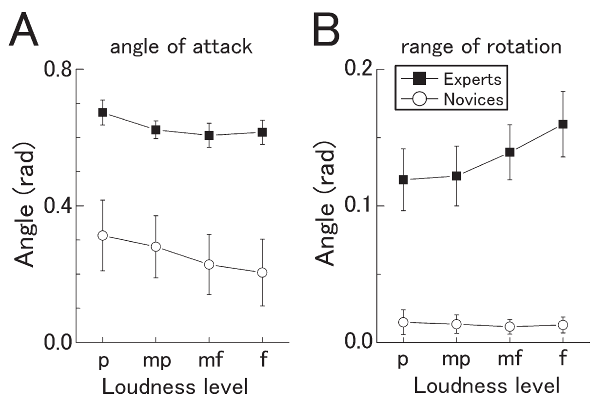

Fig. 7. The group means of the angle of attack at the key-bottom moment (A), and the range of its angular rotation during the key-depression phase (B). The error bars represent±1 S.E.

joint because proximal segments have a higher inertia and more massive musculature than the distal segments (see Putnam, 1993). Our findings support and extend this idea. For experts, a large shoulder extension deceleration by the flexion NET produced powerful INTs at the elbow and wrist joints. In addition, the magnitude of these torques increased when eliciting a louder tone. The shoulder joint thus served as a leading joint for them. For novices, on the other hand, the magnitude of both the shoulder flexion NET and elbow extension INT was close to zero across all loudness levels. Our earlier study of keystroke motion by novices demonstrated that the magnitude of forearm deceleration increased with an increase in the level of loudness (Furuya and Kinoshita, 2008). This must have contributed to a loudness-dependent increase in the wrist flexion INT in the present study. Therefore, the elbow joint could be their leading joint. These findings indicate that the leading–subordinate relationship changes with training toward the use of a more powerful source for the production of larger INTs in order to decrease the muscular work at the distal joints.

The movement organization of the novices in which INTs were much less effectively used for the movement of the distal limbs due to the disuse of the shoulder as the leading joint at all keystroke velocities may merit further discussion. According to Putnam (1993), in order to effectively exploit INTs, a complex temporal scheduling of rotational deceleration beginning from the most proximal joint to the more distal joint is required. Indeed, our previous study comparing the movement timing of the upper limb segments during the same keystroke motion between expert and novice piano players showed that this was the case in experts but not in novices (Furuya and Kinoshita, 2007). A simulation study of the ball-throw motion demonstrated that even a small change of as much as several tens of milliseconds in the onset time of proximal joint deceleration could modulate both the magnitude and direction of the resulting INTs at the distal joints significantly enough to affect the normal throwing motion (Hirashima et al., 2003b). The effective use of INTs thus requires preprogramming and controlling the precise timing and magnitude of MUS production to appropriately decelerate the proximal joint, which could have been a difficult task for the novices. Indeed, the acquisition of such a multi-joint movement pattern that the proximal joint deceleration precedes that of the distal joint requires training (Buchanan, 2004). Instead, novices could have selected an easier control strategy in which the movement of the shoulder joint was temporally coupled with more distal joints. Indeed, this appears to be the case when throwing a ball by the non-dominant arm (Hore et al., 2005).

The amount of INT generated at the MP joint was fairly small and did not differ between the experts and novices. A greater level of INT to facilitate finger flexion was therefore not a necessary component of skillful keystroke motion. This appears to be reasonable because the production of flexion INT at the MP joint of striking fingers requires decelerating the hand descending motion, which simultaneously produces flexion INTs at the non-striking fingers. In order to avoid sounding by these fingers, therefore, exerting additional muscular effort to offset the INTs at these fingers would become necessary. This would be not only physiologically inefficient, but also constrains the independent control of the fingers, an important skill in playing the piano (Aoki et al., 2005).

Reduction of key reaction force torque with achievement of higher angle of attack

The findings of the present study showed that the REA and MUS at the MP joint were smaller for the experts as compared with the novices. This can be suitably explained by the findings of the hand placement with a closer MP joint center to the key reaction force vector for experts as compared with novices. Consistent with our previous observation (Furuya and Kinoshita, 2008), this was accomplished by forming a hand posture with a larger orientation angle of the finger relative to the key ("angle of attack"). The experts achieved a larger angle of attack by using a vigorous shoulder flexion motion during key depression, which was not apparent in the novices. The development

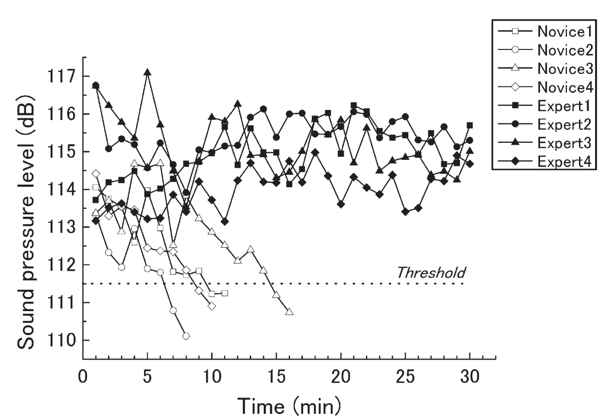

Fig. 8. Results of the endurance test for repetitive piano keystrokes. The black and white symbols represent an expert and a novice piano player, respectively. The horizontal dotted line indicates the lowest boundary of the target SPL (111.5 dB) for the determination of muscular fatigue.

of a large shoulder flexion MUS toward the end of key depression for the experts would therefore be used for configuring the hand posture with the intention of reducing the finger muscular effort for offsetting the perturbing effects of the key-force. This may imply that unlike more proximal joints, the experts preferably benefit from the geometrical features of the limb rather than the dynamic property of the limb in order to reduce the muscular effort exerted by the fingers. Although previous studies suggested that the geometrical configuration of the upper-limb is taken into account when planning multi-joint movements that involve a mechanical interaction with objects (Lacquaniti et al., 1992; Sabes et al., 1998; Santello, 2005), to the best of our knowledge, this is the first study that has provided data indicating that expertise allows for taking better advantage of the arm/hand configuration in order to reduce the muscular work.

The present findings also indicated that reduction of the REA at the MP joint required incorporating the shoulder flexion as an additional degree of freedom (DOFs) into the keystroke motion. However, an increase in DOFs commonly leads to greater complexity of computation for kinematic planning as well as inverse dynamics in multi-joint movements (Atkeson, 1989; Yang et al., 2007). In order to reduce these complexities, the novices might have selected a simplified control strategy in which the movement of all joints was temporally coupled and shoulder flexion was not incorporated into movement production. Kinematic findings for the present novices with a fairly small amount of shoulder flexion indeed strongly supported this possibility.

Benefits of organizing the keystroke motion with the use of interaction torques and reduction in key reaction torque

There appear to be at least two benefits of organizing keystroke on the piano with the use of INTs and reduction of REA; attaining a higher physiological efficiency and reducing movement errors. Playing the piano generally requires a number of repetitive force productions by the upper-limb MUSs for a prolonged period. In order to maintain fine motor performance and decrease the risk of playing-related injuries (Furuya et al., 2006b), it is essential to avoid muscular fatigue. According to Herzog (2000), the endurance of the MUSs to fatigue is proportional to the physiological cross-sectional area (PCSA). In addition, our motor system has a common anatomical architecture in which more distal MUSs have a smaller PCSA. Therefore, our finding that the experts had smaller MUSs at the elbow, wrist, and MP joints, and a larger MUS at the shoulder as compared with the novices can be interpreted in terms of the CNS's planning of the keystroke motion to minimize muscular fatigue during playing the piano (see Fig. 8). A feasibility of this view was further strengthened by the report from the present novice players who all claimed that they failed to continue the endurance test due to exhaustion of the hand and/or forearm MUSs. Studies have shown that a similar strategy is commonly used in walking, running, and cycling, in which the CNS is likely to account for the minimization of muscular fatigue (Dul et al., 1984a,b; Srinivasan and Ruina, 2006; Prilutsky and Zatsiorsky, 2002).

The greater reliance on the proximal MUS and reduced contribution of the distal MUS for the experts can also be related to the increase in the movement accuracy, as indicated by their lower values of CV of key descending force and velocity. Jones et al. (2002) have shown that the total noise affecting the activation of each MUS increases approximately linearly with the amplitude of the motor command signal. Hamilton et al. (2004) examined the signal-dependent noise of MUSs with different strengths during an isometric force production task and found that a given torque or force can be more accurately generated by a stronger MUS than a weaker MUS. By increasing the MUS at the proximal (stronger) MUSs and decreasing the MUS at the distal (weaker) MUSs, the negative effects of signal-dependent noise on the endpoint movement can be minimized. By this mechanism, delicate musical expressions would be ensured when experts play the piano. This appears to support the idea of optimal control of the endpoint movement variance in a target-aiming task (Harris and Wolpert, 1998).

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APPENDIX

Equations of motion of the four linked segment model

Shoulder

$$\mathrm{NET}=\ddot{\varphi}_1\left[\begin{array}{l} I_1+I_2+I_3+I_4+m_1r_1^2+m_2\left(l_1^2+r_2^2\right) \\ \quad +m_3\left(l_1^2+l_2^2+r_3^2\right)+m_4\left(l_1^2+l_2^2+l_3^2+r_4^2\right) \\ +2\left(m_2r_2l_1+m_3l_1l_2+m_4l_1l_2\right)\times\cos\varphi_2 \\ +2\left(m_3r_3l_1+m_4l_1l_3\right)\cos\left(\varphi_2+\varphi_3\right) \\ +2\left(m_4r_4l_1\right)\cos\left(\varphi_2+\varphi_3+\varphi_4\right) \\ +2\left(m_3r_3l_2+m_4l_2l_3\right)\cos\varphi_3+2\left(m_4r_4l_2\right) \\ \cos\left(\varphi_3+\varphi_4\right)+2\left(m_4r_4l_3\right)\cos\varphi_4 \end{array}\right]$$

$$\mathrm{INT}=-\ddot{\varphi}_2\left[\begin{array}{l} I_2+I_3+I_4+m_2(l_1^2+r_2^2)+m_3(l_1^2+l_2^2+r_3^2) \\ +m_4(l_1^2+l_2^2+l_3^2+r_4^2) \\ +\left(m_2r_2l_1+m_3l_1l_2+m_4l_1l_2\right)\cos\varphi_2 \\ +\left(m_3r_3l_1+m_4l_1l_3\right)\cos\left(\varphi_2+\varphi_3\right) \\ +\left(m_4r_4l_1\right)\cos(\varphi_2+\varphi_3+\varphi_4) \\ +2\left(m_3r_3l_2+m_4l_2l_3\right)\cos\varphi_3 \\ +2\left(m_4r_4l_2\right)\cos\left(\varphi_3+\varphi_4\right)+2\left(m_4r_4l_3\right)\cos\varphi_4 \end{array}\right]$$

$$-\ddot{\varphi}_3\left[\begin{array}{l} I_3+I_4+m_3(l_1^2+l_2^2+r_3^2)+m_4(l_1^2+l_2^2+l_3^2+r_4^2) \\ +(m_3r_3l_1+m_4l_1l_3)\cos(\varphi_2+\varphi_3) \\ +(m_4r_4l_1)\cos(\varphi_2+\varphi_3+\varphi_4) \\ \qquad +(m_3r_3l_2+m_4l_2l_3)\cos \\ \varphi_3+(m_4r_4l_2)\cos(\varphi_3+\varphi_4)+2(m_4r_4l_3)\cos\varphi_4 \end{array}\right]$$

$$-\ddot{\varphi}_4\left[\begin{array}{l} I_4+m_4r_4^2+(m_4r_4l_3)\cos\varphi_4 \\ +(m_4r_4l_2)\cos(\varphi_3+\varphi_4) \\ +(m_4r_4l_1)\cos(\varphi_2+\varphi_3+\varphi_4) \end{array}\right]$$

$$-\dot{\varphi}_2^2\left[\begin{array}{l} (m_2r_2l_1+m_3l_1l_2+m_4l_1l_2)\sin\varphi_2 \\ +(m_3r_3l_1+m_4l_1l_3)\sin(\varphi_2+\varphi_3) \\ +(m_4r_4l_1)\sin(\varphi_2+\varphi_3+\varphi_4) \end{array}\right]$$

$$+\dot{\varphi}_3^2\left[\begin{array}{l} (m_3r_3l_1+m_4l_1l_3)\sin(\varphi_2+\varphi_3) \\ +(m_4r_4l_1)\sin(\varphi_2+\varphi_3+\varphi_4) \\ +(m_3r_3l_2+m_4l_2l_3)\sin\varphi_3 \\ +(m_4r_4l_2)\sin(\varphi_3+\varphi_4) \end{array}\right]$$

$$+\dot{\varphi}_4^2\left[\begin{array}{l} (m_4r_4l_3)\sin\varphi_4+(m_4r_4l_2)\sin(\varphi_3+\varphi_4) \\ +(m_4r_4l_1)\sin(\varphi_2+\varphi_3+\varphi_4) \end{array}\right]$$

$$+\dot{\varphi}_1\dot{\varphi}_2\left[\begin{array}{l} 2(m_2r_2l_1+m_3l_1l_2+m_4l_1l_2)\sin\varphi_2 \\ +2(m_3r_3l_1+m_4l_1l_3)\sin(\varphi_2+\varphi_3) \\ +2(m_4r_4l_1)\sin(\varphi_2+\varphi_3+\varphi_4) \end{array}\right]$$

$$+\dot{\varphi}_1\dot{\varphi}_3\left[\begin{array}{l} 2(m_3r_3l_2+m_4l_2l_3)\sin\varphi_3 \\ +2(m_3r_3l_1+m_4l_1l_3)\sin(\varphi_2+\varphi_3) \\ +2(m_4r_4l_2)\sin(\varphi_3+\varphi_4) \\ +2(m_4r_4l_1)\sin(\varphi_2+\varphi_3+\varphi_4) \end{array}\right]$$

$$+\dot{\varphi}_1\dot{\varphi}_4\left[\begin{array}{l} 2(m_4r_4l_3)\sin\varphi_4+2(m_4r_4l_2)\sin(\varphi_3+\varphi_4) \\ +2(m_4r_4l_1)\sin(\varphi_2+\varphi_3+\varphi_4) \end{array}\right]$$

$$+\dot{\varphi}_2\dot{\varphi}_3\left[\begin{array}{l} 2(m_3r_3l_2+m_4l_2l_3)\sin\varphi_3 \\ +2(m_3r_3l_1+m_4l_1l_3)\sin(\varphi_2+\varphi_3) \\ +2(m_4r_4l_2)\sin(\varphi_3+\varphi_4) \\ +2(m_4r_4l_1)\sin(\varphi_2+\varphi_3+\varphi_4) \end{array}\right]$$

$$+\dot{\varphi}_2\dot{\varphi}_4\left[\begin{array}{l} 2(m_4r_4l_3)\sin\varphi_4+2(m_4r_4l_2)\sin(\varphi_3+\varphi_4) \\ +2(m_4r_4l_1)\sin(\varphi_2+\varphi_3+\varphi_4) \end{array}\right]$$

$$-\dot{\varphi}_3\dot{\varphi}_4\left[\begin{array}{l} 2(m_4r_4l_3)\sin\varphi_4 \\ +2(m_4r_4l_2)\sin(\varphi_3+\varphi_4) \\ +2(m_4r_4l_1)\sin(\varphi_2+\varphi_3+\varphi_4) \\ +(m_4r_4l_2)\cos(\varphi_3+\varphi_4)+2(m_4r_4l_3)\cos\varphi_4 \end{array}\right]$$

$$\mathrm{GRA}=-g\left[\begin{array}{l} (m_1r_1+m_2l_1+m_3l_1+m_4l_1)\sin\varphi_1 \\ +(m_2r_2+m_3l_2+m_4l_2)\sin(\varphi_1+\varphi_2) \\ +(m_3r_3+m_4l_3)\sin(\varphi_1+\varphi_2+\varphi_3) \\ +(m_4r_4)\sin(\varphi_1+\varphi_2+\varphi_3+\varphi_4) \end{array}\right]$$

$$\mathrm{REA}=F\left[\begin{array}{l} l_1\cos\varphi_1+l_2\cos(\varphi_1+\varphi_2)+l_3\cos(\varphi_1+\varphi_2+\varphi_3) \\ +l_4\ (\varphi_1+\varphi_2+\varphi_3+\varphi_4) \end{array}\right]$$

$$\mathrm{MUS}=\mathrm{NET}-\mathrm{INT}-\mathrm{GRA}-\mathrm{REA}$$

Elbow

$$\mathrm{NET}=\ddot{\varphi}_2\left[\begin{array}{l} I_2+I_3+I_4+m_2r_2^2+m_3(l_2^2+r_3^2)+m_4(l_2^2+l_3^2+r_4^2) \\ +2(m_3r_3l_2+m_4l_2l_3)\cos\varphi_3+2(m_4r_4l_2)\cos(\varphi_3+\varphi_4) \\ +2(m_4r_4l_3)\cos\varphi_4 \end{array}\right]$$

$$\mathrm{INT}=-\ddot{\varphi}_1\left[\begin{array}{l} I_2+I_3+I_4+m_2r_2^2+m_3(l_2^2+r_3^2)+m_4(l_2^2+l_3^2+r_4^2) \\ +(m_2r_2l_1+m_3l_1l_2+m_4l_1l_2)\cos\varphi_2 \\ +(m_3r_3l_1+m_4l_1l_3)\cos(\varphi_2+\varphi_3) \\ +(m_4r_4l_1)\cos(\varphi_2+\varphi_3+\varphi_4) \\ +2(m_3r_3l_2+m_4l_2l_3)\cos\varphi_3 \\ +2(m_4r_4l_2)\cos(\varphi_3+\varphi_4)+2(m_4r_4l_3)\cos\varphi_4 \end{array}\right]$$

$$-\ddot{\varphi}_3\left[\begin{array}{l} I_3+I_4+m_3r_3^2+m_4(l_3^2+r_4^2) \\ +(m_3r_3l_2+m_4l_2l_3)\cos\varphi_3 \\ +(m_4r_4l_2)\cos(\varphi_3+\varphi_4)+2(m_4r_4l_3)\cos\varphi_4 \end{array}\right]$$

$$-\ddot{\varphi}_4\left[I_4+m_4r_4^2+(m_4r_4l_2)\cos(\varphi_3+\varphi_4)+(m_4r_4l_3)\cos\varphi_4\right]$$

$$-\dot{\varphi}_1\left[\begin{array}{l} (m_2r_2l_1+m_3l_1l_2+m_4l_1l_2)\sin\varphi_2 \\ +(m_3r_3l_1+m_4l_1l_3)\sin(\varphi_2+\varphi_3) \\ +(m_4r_4l_1)\sin(\varphi_2+\varphi_3+\varphi_4) \end{array}\right]$$

$$+\dot{\varphi}_3\left[(m_3r_3l_2+m_4l_2l_3)\sin\varphi_3+(m_4r_4l_2)\sin(\varphi_3+\varphi_4)\right]$$

$$+\dot{\varphi}_4\left[(m_4r_4l_3)\sin\varphi_4+(m_4r_4l_2)\sin(\varphi_3+\varphi_4)\right]$$

$$+\dot{\varphi}_1\dot{\varphi}_3\left[2(m_3r_3l_2+m_4l_2l_3)\sin\varphi_3+2(m_4r_4l_2)\sin(\varphi_3+\varphi_4)\right]$$

$$+\dot{\varphi}_1\dot{\varphi}_4\left[2(m_4r_4l_3)\sin\varphi_4+2(m_4r_4l_2)\sin(\varphi_3+\varphi_4)\right]$$

$$+\dot{\varphi}_2\dot{\varphi}_3\left[2(m_3r_3l_2+m_4l_2l_3)\sin\varphi_3+2(m_4r_4l_2)\sin(\varphi_3+\varphi_4)\right]$$

$$+\dot{\varphi}_2\dot{\varphi}_4\left[2(m_4r_4l_3)\sin\varphi_4+2(m_4r_4l_2)\sin(\varphi_3+\varphi_4)\right]$$

$$+\dot{\varphi}_3\dot{\varphi}_4\left[2(m_4r_4l_3)\sin\varphi_4+2(m_4r_4l_2)\sin(\varphi_3+\varphi_4)\right]$$

$$\mathrm{GRA}=-g\left[\begin{array}{l} (m_2r_2+m_3l_2+m_4l_2)\sin(\varphi_1+\varphi_2) \\ +(m_3r_3+m_4l_3)\sin(\varphi_1+\varphi_2+\varphi_3) \\ +(m_4r_4)\sin(\varphi_1+\varphi_2+\varphi_3+\varphi_4) \end{array}\right]$$

$$\mathrm{REA}=F\left[\begin{array}{l} l_2\cos(\varphi_1+\varphi_2)+l_3\cos(\varphi_1+\varphi_2+\varphi_3) \\ +l_4\cos(\varphi_1+\varphi_2+\varphi_3+\varphi_4) \end{array}\right]$$

$$\mathrm{MUS}=\mathrm{NET}-\mathrm{INT}-\mathrm{GRA}-\mathrm{REA}$$

Wrist

$$\mathrm{NET}=\ddot{\varphi}_3\left[I_3+I_4+m_3r_3^2+m_4(l_3^2+r_4^2)+2(m_4r_4l_3)\cos\varphi_4\right]$$

$$\mathrm{INT}=-\ddot{\varphi}_1\begin{bmatrix} I_3+I_4+m_3r_3^2+m_4(l_3^2+r_4) \\ +(m_3r_3l_1+m_4l_1l_3)\cos(\varphi_2+\varphi_3) \\ +(m_4r_4l_1)\cos(\varphi_2+\varphi_3+\varphi_4) \\ +(m_3r_3l_2+m_4l_2l_3)\cos\varphi_3 \\ +(m_4r_4l_2)\cos(\varphi_3+\varphi_4) \\ +2(m_4r_4l_3)\cos\varphi_4 \end{bmatrix}$$

$$-\ddot{\varphi}_2\begin{bmatrix} I_3+I_4+m_3r_3+m_4(l_3+r_4) \\ +(m_3r_3l_2+m_4l_3l_3)\cos\varphi_3 \\ +(m_4r_4l_2)\cos(\varphi_3+\varphi_4)+2(m_4r_4l_3)\cos\varphi_4 \end{bmatrix}$$

$$-\ddot{\varphi}_4[I_4+m_4r_4+(m_4r_4l_3)\cos\varphi_4]$$

$$-\dot{\varphi}_1\begin{bmatrix} (m_3r_3l_1+m_4l_1l_3)\sin(\varphi_2+\varphi_3) \\ +(m_4r_4l_1)\sin(\varphi_2+\varphi_3+\varphi_4) \\ +(m_3r_3l_2+m_4l_2l_3)\sin\varphi_3 \\ +(m_4r_4l_2)\sin(\varphi_3+\varphi_4) \end{bmatrix}$$

$$-\dot{\varphi}_2[(m_3r_3l_2+m_4l_2l_3)\sin\varphi_3+(m_4r_4l_2)\sin(\varphi_3+\varphi_4)]$$

$$+\dot{\varphi}_4[(m_4r_4l_3)\sin\varphi_4]$$

$$-\dot{\varphi}_1\dot{\varphi}_2\begin{bmatrix} 2(m_3r_3l_2+m_4l_2l_3)\sin\varphi_3 \\ +2(m_4r_4l_2)\sin(\varphi_3+\varphi_4) \end{bmatrix}$$

$$+\dot{\varphi}_1\dot{\varphi}_4[2(m_4r_4l_3)\sin\varphi_4]$$

$$+\dot{\varphi}_2\dot{\varphi}_4[2(m_4r_4l_3)\sin\varphi_4]$$

$$+\dot{\varphi}_3\dot{\varphi}_4[2(m_4r_4l_3)\sin\varphi_4]$$

$$\mathrm{GRA}=-g\begin{bmatrix} (m_3r_3+m_4l_3)\sin(\varphi_1+\varphi_2+\varphi_3) \\ +(m_4r_4)\sin(\varphi_1+\varphi_2+\varphi_3+\varphi_4) \end{bmatrix}$$

$$\mathrm{REA}=F[l_3\cos(\varphi_1+\varphi_2+\varphi_3)+l_4\cos(\varphi_1+\varphi_2+\varphi_3+\varphi_4)]$$

$$\mathrm{MUS}=\mathrm{NET}-\mathrm{INT}-\mathrm{GRA}-\mathrm{REA}$$

MP

$$\mathrm{NET}=\ddot{\varphi}_4[I_4+m_4r_4^2]$$

$$\mathrm{INT}=-\ddot{\varphi}_1\begin{bmatrix} I_4+m_4r_4^2+(m_4r_4l_1)\cos(\varphi_2+\varphi_3+\varphi_4) \\ +(m_4r_4l_3)\cos\varphi_4+(m_4r_4l_1)\cos(\varphi_3+\varphi_4) \end{bmatrix}$$

$$-\ddot{\varphi}_2\begin{bmatrix} I_4+m_4r_4^2+(m_4r_4l_2)\cos(\varphi_3+\varphi_4) \\ +(m_4r_4l_3)\cos\varphi_4 \end{bmatrix}$$

$$-\ddot{\varphi}_3[I_4+m_4r_4^2(m_4r_4l_3)\cos\varphi_4]$$

$$-\dot{\varphi}_2^{1}\begin{bmatrix} (m_4r_4l_1)\sin(\varphi_2+\varphi_3+\varphi_4) \\ +(m_4r_4l_3)\sin\varphi_4+(m_4r_4l_2)\sin(\varphi_3+\varphi_4) \end{bmatrix}$$

$$-\dot{\varphi}_2^2[(m_4r_4l_3)\sin\varphi_4+(m_4r_4l_2)\sin(\varphi_3+\varphi_4)]$$

$$-\dot{\varphi}_3^2[(m_4r_4l_3)\sin\varphi_4]$$

$$-\dot{\varphi}_1\dot{\varphi}_2[2(m_4r_4l_3)\sin\varphi_4+2(m_4r_4l_2)\sin(\varphi_3+\varphi_4)]$$

$$-\dot{\varphi}_1\dot{\varphi}_3[2(m_4r_4l_3)\sin\varphi_4]$$

$$-\dot{\varphi}_2\dot{\varphi}_3[2(m_4r_4l_3)\sin\varphi_4]$$

$$\mathrm{GRA}=-g[(m_4r_4)\sin(\varphi_1+\varphi_2+\varphi_3+\varphi_4)]$$

$$\mathrm{REA}=F[l_4\cos(\varphi_1+\varphi_2+\varphi_3+\varphi_4)]$$

$$\mathrm{MUS}=\mathrm{NET}-\mathrm{INT}-\mathrm{GRA}-\mathrm{REA}$$

SYMBOLS. I_i=moment of inertia about the center of GRA, r_i=distance to center of GRA from proximal joint of the segment, l_i=length, m_i=mass (i=1: upper arm, 2: forearm, 3: hand, 4: finger). The hand was defined as a portion from the wrist joint center to MP joint center, while the finger was from the MP joint center to the fingertip. φ_i=Joint angle (i=1: shoulder, 2: elbow, 3: wrist, 4: MP). To approximate the sum of key reaction forces applied at the thumb and little finger, the measured key reaction force were doubled and inputted into the value of F in equations of motion (Furuya and Kinoshita, 2007). The tangential force was set to nil for simplicity of computation.

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