Hand kinematics of piano playing

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Dexterous use of the hand represents a sophisticated sensorimotor function. In behaviors such as playing the piano, it can involve strong temporal and spatial constraints. The purpose of this study was to determine fundamental patterns of covariation of motion across joints and digits of the human hand. Joint motion was recorded while five expert pianists played thirty excerpts from musical pieces, which featured about fifty different tone sequences and fingering. Principal component analysis and cluster analysis using an expectation-maximization algorithm revealed that joint velocities could be categorized into several patterns, which help to simplify the description of the movements of the multiple degrees of freedom of the hand. For the thumb keystroke, two distinct patterns of joint movement covariation emerged and they depended on the spatiotemporal patterns of the task. For example, the thumb-under maneuver was clearly separated into two clusters based on the direction of hand translation along the keyboard. While the pattern of the thumb joint velocities differed between these clusters, the motions at the MCP and PIP joints of the four fingers were more consistent. For a keystroke executed with one of the fingers, there were three distinct patterns of joint rotations, across which motion at the striking finger was fairly consistent, but motion of the other fingers was more variable. Furthermore, the amount of movement spillover of the striking finger to the adjacent fingers was small irrespective of the finger used for the keystroke. These findings describe an unparalleled amount of independent motion of the fingers.
Playing the piano represents one of the most accomplished movements in our repertoire. Production of a wide variety of tone sequences requires coordination and individuation of movements across digits and extensive piano training may elicit anatomical and functional changes (Münte et al. 2002) in brain regions responsible for hand movements such as motor cortex (Amunts et al. 1997; Jäncke et al. 2000) and cerebellum (Gaser and Schlaug 2003; Koeneke et al. 2004). Yet, this plasticity has a potential risk of causing neurological disorders such as focal hand dystonia, which is characterized by unwanted spill-over of movement from the intended digit to non-intended digits and involuntary coactivation at the hand muscles (Hallett 2011). Understanding the organization of hand movements in piano playing is therefore useful not only to provide insight to the neural control of skilled hand behaviors but also to provide a basis for studying neurological disorders exacerbating hand motor functions.

Studies of the kinematics of finger movements in a variety of tasks have demonstrated strategies that involve covariation of motion across joints and fingers (Schieber and Santello 2004). Such synergies manifest themselves during motor tasks such as grasping (Santello et al., 1998, 2002; Mason et al., 2001), typing (Soechting and Flanders 1997), finger-spelling (Klein Breteler et al. 2007), and haptic exploration (Thakur et al. 2008). These studies observed that a few patterns of covariation accounted for the majority of variability across different movements. One movement pattern common among most of these tasks was
motion at multiple fingers in the same direction, compatible with anatomical and neural coupling across digits (Lang and Schieber 2004).

A recent study using transcranial magnetic stimulation (TMS) showed that the pattern of finger movements evoked by stimulating motor cortex during rest differed between pianists and non-musicians (Gentner et al. 2010). Also, TMS stimulation of motor regions innervating a hand muscle evoked simultaneous activation of other muscles more strongly for pianists than for non-musicians (Rosenkranz et al. 2009). One may therefore expect stronger spillover of movements at one digit to adjacent fingers while playing the piano. By contrast, a conflicting result was provided by behavioral studies using finger tapping, which demonstrated that pianists restricted force production at non-tapping digits more precisely than musically-untrained individuals (Aoki et al. 2005; Parlitz et al. 1998). This raised an alternative possibility of augmented inhibition of spillover of movements by pianists. To date, however, it is not known whether hand movements during piano playing can be characterized either by more coupled or by more individuated motions.

The present study was aimed at defining the fundamental patterns of covariation in joint rotations underlying the rich repertoire of hand movements during piano playing by recording dynamic changes in hand posture while expert pianists played various musical pieces. When the keypress was executed with the thumb, we found patterns of correlated motion of the four fingers that were associated
with two distinct patterns of the thumb’s motion. By contrast, keypresses executed with the fingers were characterized by highly individuated digit motions.

METHODS

Subjects

Five highly-skilled pianists (2 female, 3 male, 33±8 yrs, all right-handed) participated in our experiment after giving informed consent for the study. All of them won prizes at international and/or national piano competitions. The experimental protocol was approved by the University of Minnesota’s Institutional Review Board.

Experimental Design

We asked subjects to play several measures of eleven musical pieces requiring use of the right hand. The selections chosen were thirty short excerpts ranging from 9 to 24 notes (mean ± SD = 13.5 ± 2.8) from eleven pieces, which were “Étude Op. 10 No. 1, 4, 8 and Op. 25 No. 11, 12” by Frédéric Chopin, “Das wohltemperierte Klavier, Vol. 1 No. 15 and Vol. 2 No. 1, 2, 10, 15” by Johann Sebastian Bach, and “15 Études Op. 72 No. 6” by Moritz Moszkowski (see Fig. 1 which shows excerpts from each of the three composers). These pieces were chosen so that all possible combination of fingerings should be used. Namely, they included (1) fingerings in which preceding and subsequent keystrokes of the keypress with one digit were performed by one of the other four digits, and (2) several different key
positions played with the same fingering. None of the sequences involved repetitive use of the same digit, which would require lifting a digit prior to and following a keypress. All notes were sixteenth notes, and chords were eliminated. The fingering was specified on each score presented so that all players would use the same finger patterns for the same pieces of music (Fig. 1). The pianists played a digital piano (Roland ep-5, 61 keys), connected to a Windows computer (SONY VAIO VGN-Z90PS) via a MIDI interface (Roland EDIROL UA-4FX). They were provided with the score for each of the pieces on a computer monitor located in front of the piano, and were allowed practice to familiarize themselves with the piano and with the musical selection. During practice, subjects played until they felt that they could play consistently and accurately without making mistakes.

Subjects were asked to play each of the thirty excerpts for 10 successful trials at a certain tempo. The tempo was provided by a metronome (inter-keystroke interval = 125 msec), and subjects played in synchrony with the metronome. This tempo is one at which pianists normally play these pieces. All pieces were played with legato touch, meaning that a key was not released until the next key was depressed.

Subjects were asked to play at the loudness of 100 MIDI velocity.

Data Acquisition

We recorded the subjects’ hand postures dynamically using sensors embedded in a right-handed
glove (CyberGlove, Virtual Technologies, Palo Alto, CA). The glove fit tightly but was thin and flexible
and open at the fingertips. We recorded the motions at 17 degrees of freedom with angular resolution
<0.5°, at 12 msec intervals (Jerde et al. 2003; Santello et al. 2002). The measured angles were the
metacarlo-phalangeal (MCP) and proximal-phalangeal (PIP) joint angles of the four fingers as well as the
angles of abduction (abd) between adjacent fingers. For the thumb, the MCP, abd and interphalangeal (IP)
angles were measured, as was the angle of thumb rotation (ROT) about an axis passing through the
trapeziometacarpal joint of the thumb and index MCP joint. Two additional degrees of freedom defined
wrist rotation, which was not considered in our analysis. Flexion and abduction were defined as positive;
the MCP and PIP angles were defined as 0 when the finger was straight and in the plane of the palm. At
the thumb, positive values of thumb rotation denoted internal rotation.

We also recorded MIDI data from the keyboard by using a custom-made script in LabVIEW
(National Instruments), running at 200 Hz in synchronization with the CyberGlove (Furuya and Soechting
2010). From MIDI data, we derived information on the velocity with which each key was depressed
(loudness) and on the time the key was depressed (Engel et al. 1997). Using this information, each
inter-keystroke interval was time normalized as 100 samples, so as to minimize inter-trial and
inter-subject variability in timing. Consequently, the normalized times of keypress occur at times -200,
-100, 0, +100, +200 (see Fig. 3).
Data Analysis

We analyzed a sequence of five successive strokes having a particular keypress with each of the five digits at the center of the sequence. From 30 music excerpts, we obtained in total 64, 64, 49, 56, and 51 patterns of tone sequences played with a variety of key positions requiring different fingerings for the keypress with the thumb, index, middle, ring and little finger, respectively. For the data during the thumb keypress, there were two distinct types of movement depending on whether or not the thumb keypress involved a “thumb-under” maneuver, in which the thumb moved under the fingers to facilitate translation of the hand along the keyboard (Engel et al. 1997). This maneuver is of particular importance in piano playing that requires smooth transition of fingertip position over time in a relatively large workspace. The rightward thumb-under involves the thumb internal rotation prior to the thumb keypress, followed by external rotation while the thumb was depressing the key so as to reach a higher note with the fingers, whereas the leftward thumb-under involves the thumb internal rotation during the key-depression to reach a lower key with the fingers. The number of tone sequences with and without the thumb-under was 15 and 49, respectively. Representative tone sequences are shown in Figure 2.

Figure 2 inserted here

Principal Component Analysis

In order to describe patterns of coordination among various degrees of freedom at the hand, we
performed principal component (PC) analysis. The PC analysis determined patterns of covariation of
time-varying joint kinematics across tone sequences, which allowed for determining the movement
templates to reconstruct a variety of finger movements. This is conceptually similar to the time-varying
muscle synergy analysis described by d’Avella and Bizzi (2005).

The PC analysis we used was one that was developed in previous studies (Klein Breteler et al.
2007; Santello et al. 2002). The input to our time-varying synergy PC analysis was the averaged angular
velocity for each joint, for each tone sequence, during the time interval of five successive strokes (2
keypresses before and after the particular keystroke with each finger). Each of the tone sequence vectors
consisted of a series of 15 joint velocity waveforms. We did a separate analysis for the tone sequences
centered on each of the 5 digits, for each of the 5 subjects.

The PC waveform analysis that we used in the present study was the type mentioned by Glaser
and Ruchkin (1976). This analysis results in n basic PC waveforms, computed from the n × n covariance
matrix of the n tone-sequence vectors (n ranging from 49 to 64). The covariance calculation removes the
mean from each of the n columns of the input matrix. Thus, the angular velocity waveforms at each joint
for each tone sequence (400 time units for each joint) could be perfectly reconstructed as the average
angular velocity at a $j^{th}$ joint for $i^{th}$ tone sequence ($\text{mean } \dot{\theta}_j^i$) plus a weighted sum of the n PC waveforms
($\text{PC}_j^{1...n}$) at a $j^{th}$ joint:

\[ \hat{\theta}_i = \text{mean} \hat{\theta}_i + PC^{1^i} \times W_{1i} + \cdots + PC^{n^i} \times W_{ni} \] 

where \( W_{1i} - W_{ni} \) are the weighting coefficients for a \( i^{th} \) tone sequence. The PCs are ranked such that PC1 accounts for the largest portion of the variance.

Comparison of PCs across subjects

To quantitatively determine the correspondence of PCs across subjects, we compared two sets of PCs extracted from different subjects by performing a linear regression analysis between the PC waveforms. We matched pairs of PCs starting with the pair with the highest R-squared value, removing the PCs of the selected pair from their respective sets, and then matching the remaining elements. The PC3 for two subjects best matched with the PC4 for the remaining three subjects, and vice versa with regard to the data during the thumb keypress. We therefore exchanged PC3 and PC4 for these two subjects so that the similarity of a given PC across subjects could be maximized. Similarly, we exchanged the PC4 and PC5 of the subject 3 for the thumb keypress, PC3 and PC4 of the subject 3 for the index keypress, PC2 and PC3 of the subject 2 for the middle keypress, PC3 and PC4 of the subject 1 and PC2 and PC3 of the subject 3 for the ring keypress, and PC2 and PC3 of the subject 4 for the little keypress.

Cluster Analysis

Using the weighting coefficients (\( W_{ni} \)) derived from the time-varying synergy PC analysis, we performed a cluster analysis using an expectation-maximization (EM) algorithm (Dempster et al. 1977)
for the data sets centered on the keypress for each of five digits for each subject separately. The aim of
this analysis was to determine whether or not a few patterns were adequate to describe coordination of
finger movements during the playing of a wide variety of sequences. We used the \( W_n \) of the first four
PCs at all tone sequences in the cluster analysis, those PCs accounting for more than 60% of the total
variance for all digits (Table 1).

For the purpose of analysis, the inputted dataset \((W_n)\) in the four dimensional hyperspace was
assumed to consist of a set of normal probability density functions. The EM algorithm was applied to
estimate these functions, using the following procedure. The probability density of a multivariate space is
assumed to be described by the superposition of a number of normal density functions (i.e. mixture of
Gaussian distributions). The parameters of the individual normal density functions are initially chosen
randomly and are then changed iteratively so that the expectation of the observed distribution increases to
a maximum. When the values of the parameters converge, the result is the best-fitting composite
probability density function for the given number of components.

The number of clusters set for the EM algorithm was 2 to 6, and for each of the numbers, the
sum of variance of the weighting coefficients within each cluster (the sum of within-cluster variance) was
computed as follows:
\[ \sigma_{\text{we}}^2 = \frac{1}{n} \sum_{c} \sum_{i} (X_i^c - \bar{X}^c)^T (X_i^c - \bar{X}^c) \]  

(2)

where \(c\) is the number of clusters (\(c=1, 2, \ldots, 6\)), \(i\) is the number of a sequence belonging to that cluster, \(n\) is the total number of sequences, and \(X\) is the vector consisting of the \(W_{ni}\) of the first four PCs. The value \((\sigma_{\text{we}}^2)\) was computed for each subject and for the keystroke with each of five digits separately, and then averaged across subjects. The average value was plotted relative to the number of clusters used for the EM. A breakpoint of the plotted curve was used to determine an optimal number of clusters for the further analysis.

We also tried a K-mean clustering but it failed to successfully segregate datasets particularly when categorizing into more than two clouds. However, this was not the case when using the EM.

Index of tone sequence

For the thumb keypress, a relatively larger change in hand posture can be involved when a thumb-under maneuver is executed. To provide a simple measure of the change of hand posture during the playing of a sequence of tones, we computed the postural-change index (PI), which is based on the right-left locations of successive keys and the digits used to strike them. The PI was computed for each sequence by using three successive keys as follows:

\[ PI = \frac{[\{(P^i - P^{i-1}) - (F^i - F^{i-1})\} + \{(P^{i+1} - P^i) - (F^{i+1} - F^i)\}]}{2} \]  

(3)

where the \(i^{th}\) keypress was always made by the thumb, and \(i-1\) and \(i+1\) keypress refer to the previous and
subsequent keystrokes executed by fingers, respectively. $P^i$ indicates the horizontal location of the key of
$i$th keypress (right is positive), and $F^i$ is the digit number that executes the $i$th keypress. The digit number is
always 1 (thumb) at the $i$th keypress, and is either 2, 3, 4, or 5 (index, middle, ring, little finger, respectively) at $i$-1 and $i$+1 strokes. The first term of PI (i.e., $\{(P^i - P^{i-1}) - (F^i - F^{i-1})\}$) reflects the posture
prior to the thumb keystroke and becomes positive when the distance between two digits used for
keypresses is larger than the distance between two keys to be struck. Therefore, this term is positive when
closing the hand prior to the thumb keypress and negative when opening the hand prior to the thumb
keypress. Here, we define closing and opening as motion that decreases and increases distance between
the thumb and four fingers, respectively. The second term of PI reflects the posture following the thumb
keypress and becomes positive when the distance between two digits used for keypresses is smaller than
the distance between two keys to be struck. Thus the second term is positive when opening the hand
following the thumb keypress. Taken together, a positive PI indicates the occurrence of a close-to-open
posture change of the hand during a course of keystrokes centered by the thumb keypress; whereas a
negative PI indicates the occurrence of an open-to-close change in hand posture. For example, in the case
of a tone sequence with the thumb-under moving left-to-right in Fig. 1, the PI value was $\{(2 - (1-3)) + \{4
- (2-1)\}/2 = (4+3)/2 = 3.5$. 

RESULTS

General observation of keystroke velocity and timing

The keystroke velocity averaged across all tone sequences had no apparent difference across subjects (99.6 ± 4.8; mean ± SD across players). Keystroke velocity was very consistent from note to note with values ranging from 98.3 ± 4.5 to 100.2 ± 5.3 for the five-note sequences analyzed. Thus there was no consistent difference in the keystroke velocity across five notes struck in succession. The velocity of a keystroke executed by the thumb, index, middle, ring and little finger was 98.9 ± 4.7 to 100.2 ± 4.8 (mean ± SD across subjects), respectively, which indicates no consistent effect of a striking digit on the keystroke velocity.

We did not perform a detailed analysis of the timing of the depression and release of the keys. Such an analysis was performed by Engel et al. (1997) who found that the time at which a particular key was depressed was very consistent from trial to trial. The timing of key release was more variable, but tended to coincide with the depression of the subsequent key for pieces played with a legato touch.

Time course of joint rotational velocities during the keystroke with thumb

We analyzed the motions of each of the digits by first separating the data according to the digit that was used to press a particular key, and then time-normalizing the data so that the interval between successive keypresses was constant and equal to 100 units. In our analysis we focused on the time interval...
that spanned ± 2 keypresses around the keypress of interest. This analysis yielded a set of waveforms at
the 15 degrees of freedom of the hand ranging from 49 to 64 tone-sequences. We found consistent
patterns of motion at the digit used to strike the key, but also to a certain extent, consistent patterns of
motion at some of the joints at adjacent digits. Furthermore, we found that the overall patterns of
responses were clustered into 2-3 characteristic patterns.

We begin by describing the pattern of joint motions when the thumb was used for the central
keypress. Our separation of analysis of thumb keystrokes from the analysis of keystrokes executed by the
other digits was motivated by the fact that the thumb played a specific role in dynamically transporting
hand position along the keyboard (i.e. thumb-under), in addition to striking a key (Engel et al. 1997). It is
useful to further subdivide movements involving the thumb keystroke according to whether or not they
involve a “thumb-under” maneuver, in which the thumb moves under the fingers to facilitate translation
of the hand along the keyboard. The thumb-under can be further separated based on the direction to
translate the hand (Fig. 2, left panel). As we will show, the patterns of coordination of joint motion tended
to be different for these different maneuvers.

For one representative pianist (subject 4), the top row of Figure 3 illustrates the average angular
velocity waveforms across all tone sequences having a thumb keypress at the center of the sequence (both
with and without the thumb-under). The next three rows show the waveforms for the first three PCs. One
inter-keystroke interval corresponds to 100 time units. Each tick (arrow) in the x-axis indicates the moment of initiation of a keypress. At the thumb, the motion consisted primarily of internal rotation and abduction (top left panel, Fig. 3). This motion was initiated one stroke before the thumb keypress (-100), and reached peak velocity at the moment of the thumb keypress (time 0). Subsequently, motion at these joints reversed direction, reaching their negative peaks around the time of the subsequent keypress (100).

There was also motion at all four fingers, with a similar time course at the MCP and PIP joints, all four fingers extending at the time of the thumb keypress. At the MCP joints, the peak velocity of extension (negative) coincided with the time of the keypress, and the extension was preceded and followed by flexion, i.e., a tri-phasic pattern. By contrast, the PIP waveforms defined a bi-phasic pattern consisting of flexion followed by extension, peak velocity in extension occurring after the keypress. Motion at the four fingers tended to be highly correlated, with an average correlation coefficient of 0.86 ± 0.06 at the MCP joint and 0.49 ± 0.29 at the PIP joint (mean ± SD across subjects). In addition, the thumb internal rotation and joint motion at the four fingers was also significantly correlated, where the average correlation coefficient was -0.79 ± 0.15 at the MCP joint and 0.20 ± 0.41 at the PIP joint. The coupled finger extension can be associated with the demand of not touching the keys during the thumb-under maneuver.

As expected, the waveforms of the average angular velocity were quite similar to those observed
in PC1 (2\textsuperscript{nd} row in Fig. 3). PC2 (3\textsuperscript{rd} row) exhibited a different, biphasic pattern of motion at the thumb, thumb external rotation being initiated two strokes before the thumb keypress and reversing to internal rotation before the thumb keypress. There was also an initial adduction of the thumb, reversing to abduction around the time of the thumb keypress. Initially, the MCP and PIP joints at the middle, ring and little fingers also underwent extension, reverting to flexion before (MCP) or at (PIP) the time of thumb keypress. Motion of the index finger differed from the motion of the other fingers. Thumb internal rotation was highly correlated with motion particularly at the ring and little fingers (average correlation coefficient of 0.77 ± 0.24 at the MCP joint and 0.56 ± 0.30 at the PIP joint). However, motion at the four fingers was less coupled in PC2 as compared to the average joint waveforms (1\textsuperscript{st} row in Fig. 2), with the average correlation coefficient being only 0.19 ± 0.29 at the MCP joint and 0.22 ± 0.42 at the PIP joint. For PC3, the thumb external rotation and MCP flexion at the ring and little fingers were initiated one stroke before the thumb keypress, and continued until the subsequent keypress.

To quantitatively evaluate the covariation of movements between the thumb and fingers during the thumb-under maneuver, we performed a linear regression analysis. We compared the waveform of the thumb internal/external rotational velocity to the waveforms of the MCP and PIP joints of all fingers. The mean slope derived from the analysis at the index, middle, ring, and little fingers was small, ranging from -0.20 ± 0.24 to 0.14 ± 0.15 for the MCP joint, and from 0.09 ± 0.24 to 0.32 ± 0.12 for the PIP joint, (mean
The mean $r^2$ value at these four fingers was also small for the MCP joint, ranging from 0.25 ± 0.09 to 0.31 ± 0.21, and somewhat larger at the PIP joint, ranging from 0.42 ± 0.15 to 0.46 ± 0.03. These results indicated that motions at the thumb and fingers were not strongly coupled during the thumb-under maneuver.

The patterns of joint motion tended to fall into two clusters. This was determined using the EM algorithm (see Methods) applied to the weighting coefficients of the PC’s. Figure 4C shows (for subject 4) that the first four PC’s accounted for more than 70% of total variance. This was representative of results for all subjects, as shown in Table 1. We used only the first 4 PC’s in the cluster analysis. Figure 4A shows the weighting coefficients (WCs) of these PC’s for each sequence with the thumb keypress in the same subject. The tone sequences have been grouped according to whether or not they included the thumb-under (TU) maneuver, and if so, according to the progression of movement (left-to-right = LR, and vice versa). We selected the number of clusters as two for the cluster analysis of the thumb keypress, because a curve representing the sum of within-cluster variance of the WCs relative to numbers of clusters qualitatively showed a breakpoint between 2 and 3 clusters (data not shown).

The tone sequences assigned to the two clusters by the analysis differed according to the direction of thumb-under (i.e. left-to-right or right-to-left), as indicated by the filled and open bars in Fig.
4A. All tone sequences with the thumb-under moving left-to-right were assigned to cluster 1, whereas those with the thumb-under moving right-to-left were in cluster 2 (Fig. 4A). A large portion of tone sequences without thumb-under were assigned to cluster 2 (77.6%) rather than cluster 1 (22.3%). Fig. 4B shows that the clustering tended to be based largely on the sign of WC2. These findings were representative of the results for all subjects, as will be shown later (i.e. Figs. 6A, D). The WC2 influenced primarily the timing of thumb joint rotation as well as the amplitude of the MCP and PIP joint motion at the fingers (see PC2 in Fig. 3).

For all tone sequences that belonged to each cluster, we reconstructed the waveforms of joint rotation based on the first four PCs and their WCs. Figure 5 illustrates the averaged waveforms of joint rotations across the sequences for each cluster for subjects 3 and 4. The waveforms were similar across these subjects and the other three subjects as well (data not shown). The most prominent difference between clusters 1 and 2 concerned the timing of peak rotational velocity of the thumb (internal rotation, MCP flexion, and abduction), which was earlier for cluster 1 (coinciding with the time of the previous keypress) than it was for cluster 2, where the peak occurred at near the time of the thumb keypress.

Figure 5 inserted here

For cluster 1, the thumb internal rotation and MCP flexion were initiated two strokes before the thumb keypress, followed by the thumb abduction. In addition, the MCP and PIP joints slightly flexed
particularly at the ring and little fingers. These rotations tended to close the hand with the thumb moving toward the palm prior to the thumb keypress. Around the moment of the thumb keypress, the thumb then began to rotate externally, with extension of the MCP and PIP joints of all fingers. These rotations were continued until the end of thumb keypress, causing the hand to open and move rightward while the key was depressed by the thumb. For cluster 2, the thumb internal rotation and abduction began later, just one stroke before the thumb keypress. Once the key started to be depressed, the thumb additionally performed MCP flexion, which moved the thumb under the palm while moving the hand leftward. In conjunction with this thumb motion, the MCP joints of the index, middle and ring fingers were simultaneously extended. During this phase, the PIP was also extended for subject 4 but was instead flexed for subject 3.

Note that both clusters showed more or less coupled joint rotation across fingers particularly at the MCP joint. The waveform was a tri-phasic pattern consisting of a series of flexion, extension and flexion. The average correlation coefficients of movements across any pair of four fingers was $0.90 \pm 0.17$ and $0.52 \pm 0.29$ at the MCP joint, and $0.51 \pm 0.30$ and $0.11 \pm 0.21$ at the PIP joint, for cluster 1 and 2, respectively.

Tone sequences were segregated into two clusters according to WC1-WC4. To assess the extent to which the composition of these clusters was consistent across all subjects, we then computed the mean value of the proportion of tone sequences without thumb-under, with left-to-right thumb-under, and with right-to-left thumb-under in each cluster (Fig. 6A). For all subjects, the tone sequences with thumb-under
were assigned into two distinct clusters depending on the movement direction. That is, the tone sequences with thumb-under moving left-to-right and right-to-left belonged to cluster 1 and 2, respectively. This result was fairly robust even when we instead used only the first two or three PCs for the cluster analysis, which confirmed that the sign of WC2 was a key determinant of these clusters.

Figure 6 inserted here

To further characterize the tone sequences belonging to each cluster, we computed the postural-change index (PI) for each tone sequence, and averaged them across all sequences belonging to each cluster (Fig. 6B). The PI showed a positive and negative value for clusters 1 and 2, respectively, which means a preceding hand-closing and/or subsequent-hand opening for the sequences in cluster 1, and vice versa in cluster 2. A t-test confirmed a significant difference between the clusters (p<0.01). We also considered PI data initially segregated according to the presence or absence of thumb-under, instead of cluster membership. For the group with thumb-under the overall pattern of hand postural change was as shown in Fig. 6B, with right-to-left thumb-under corresponding to negative PI values. For a keystroke without thumb-under, the group mean of the PI value was 1.2 ± 0.7 and -0.5 ± 0.2 for those in cluster 1 and 2, respectively, which again showed a significant difference between the clusters (t-test: p<0.01). This indicates that tone sequences without thumb-under were also separated according to pattern of change in hand posture over time; a preceding hand-closing and/or subsequent-hand opening in cluster 1, and vice
versa in cluster 2. Taken together, the PI was therefore a good predictor of cluster membership, independently of whether or not the thumb keypress involved a thumb-under maneuver. Figures 6C and D display the grand mean of WC1 and WC2 for tone sequences belonging to each of the two clusters across all 5 subjects. Among the WCs of the first four PCs, a t-test confirmed a significant difference between the two clusters only in the WC2 (p<0.01). This indicates that the clustering was thoroughly based on the sign of the WC2 for all subjects.

Time course of joint rotational velocities during the keystroke with each of the four fingers

Next, we will describe the pattern of joint motions when each of the four fingers was used for the central keystroke. In contrast to the results for the thumb, where we found a high degree of covariation of motion of the four fingers, finger motion was much more individuated when the key was struck with one of the fingers. Figure 7 illustrates the average angular velocity waveforms across all tone sequences having a keypress with each of index, middle, ring and little fingers at the center of the sequence in one subject (subject 2). The velocity at the MCP joint of the finger being used for the keypress (“striking finger”) was usually larger than the MCP joint velocity at the remaining digits. Furthermore, the MCP motion of the striking finger was generally characterized by a tri-phasic pattern that consisted of an initial extension, followed by flexion with a peak at or slightly preceding the keypress, followed by extension. The exception was the little finger, where there was a small amount of MCP flexion at the time of
keypress. There was also a small amount of extension at the PIP joint for a keystroke with any of the four fingers. Overall, the pattern of thumb motion appeared to be different for each of the finger keystrokes. For the ring finger keystroke, the thumb external rotation and adduction reached their peaks at the time of keypress. By contrast, for the index and middle finger keypresses these peaks occurred earlier.

Following the keypress, the MCP and PIP joint of the striking finger simultaneously rotated into extension and flexion, respectively, as the key was released. Note that compared with the case of thumb keystroke, joint motion covaried less across fingers at both the MCP and PIP joints. Moreover, some fingers moved in directions opposite to the motion of the striking finger. Accordingly, the average correlation coefficient between the striking and other fingers was usually negative, ranging from -0.51 to 0.09 at the MCP joint, and from -0.24 to -0.04 at the PIP joint. In addition, the MCP joint motion of the striking finger was quite similar irrespective of the finger used for keypress, with an average correlation coefficient of the MCP joint motion at the striking finger across four fingers of 0.90 ± 0.08.

Figure 7 inserted here

The magnitude of the averaged waveforms at the non-striking fingers during a keypress with each finger (Fig. 7) was small, but this resulted because the patterns of motion of the non-striking fingers differed across sequences. To determine a few characteristic and consistent patterns of motion underlying these variable motions, we did a cluster analysis. Using data from subject 2, Fig. 8 illustrates the
individual joint velocity waveforms at the MCP and PIP joints of all fingers for all tone sequences centered on the index and ring keystrokes. For the keystroke with each finger, we did the cluster analysis in the same manner as described above for the thumb keypress. Based on the results of the sum of intra-cluster variance of the first 4 PC WCs, we set the number of clusters as three due to presence of a breakpoint as the number of clusters increased from 3 to 4. A successful segregation of tone sequences is visually discernible in Fig. 8 (lines in different colors), which was also the case for the other four subjects and for the keystroke of each of the fingers.

As already evident in the averages shown in Fig. 6, the MCP joint of the striking finger consistently exhibited a tri-phasic waveform across all tone sequences (see Fig. 8). This is apparent for the keystroke of the index (top left plot, Fig. 8A) and ring (third plot, Fig. 8B) fingers. There was however some variation across clusters in the MCP motion of the striking finger, the initial MCP extension being absent or less prominent for clusters 2 and 3. This was also the case for the remaining four subjects, and for the keypress with the middle finger for all subjects. For the little finger keystroke, however, the MCP motion at the striking finger was less pronounced in all clusters, compared with the keystroke with the other fingers (see Fig. 7).

In contrast to the consistency of the MCP motion of the striking finger, motion at the MCP and
PIP joints of the adjacent fingers differed considerably across the clusters. Overall, the clusters were characterized in terms of direction of the MCP joint rotation at one previous or subsequent stroke. For example, for the index finger keystroke (Fig. 8A), in the trials in cluster 1 there was synchronous extension at the middle and ring MCP joints, paralleling the extension at the index MCP joint prior to the keypress. However, in the trials in clusters 2 and 3, there was an initial flexion at the middle MCP joint, which was not observed in the index MCP motion. During the index keystroke, motion at the index PIP joint (the striking finger) was also fairly consistent for the three clusters, whereas it differed for the middle and ring PIP joints (non-striking fingers). For each cluster, motion at the MCP joint was not well correlated between the striking and other fingers, with an average correlation coefficient of ranging from -0.12 to 0.11. In addition, motion at each of the non-striking fingers also was not correlated between the clusters, with an average correlation coefficient of 0.28 ± 0.27 at the MCP joint and 0.22 ± 0.17 at the PIP joint, which confirmed different patterns of joint motion across clusters.

The analysis for the ring finger keystroke (Fig. 8B) led to a similar conclusion. For example, in clusters 1 and 2, the index and middle MCP joints simultaneously extended, paralleling the extension at the ring MCP joint prior to the keypress. However, in the trials in cluster 3, there was an initial flexion at the index and middle MCP joints. Furthermore, motion at the ring PIP joint was consistent for the three clusters, whereas it differed for the index and middle PIP joints. For each cluster, motion at the MCP joint
was poorly correlated between the striking and other fingers, with an average correlation coefficient ranging from -0.08 to 0.30. In addition, motion at each of the non-striking fingers also was not correlated between the clusters, with an average correlation coefficient of -0.02 ± 0.29 at the MCP joint and 0.08 ± 0.25 at the PIP joint.

The lack of coupling between the motion of the striking finger and each of the non-striking fingers was also evident during keypresses with the middle and little fingers. Across all subjects, the average correlation coefficient ranged from -0.27 to 0.47 for different clusters in these instances. Joint motion at non-striking fingers also differed across clusters, with an average correlation coefficient of -0.17 ± 0.15 at the MCP joint and 0.25 ± 0.16 at the PIP joint during the middle finger keypress, and of 0.08 ± 0.31 at the MCP joint and 0.05 ± 0.30 at the PIP joint during the little finger keypress.

Figure 9 illustrates the average joint velocity waveforms across tone sequences belonging to each of the three clusters during the index and ring keystrokes by another subject (subject 5). Similar to the observation in subject 2 (Fig. 8A, B), the waveform of each joint motion differed both between fingers for each cluster and across the clusters. For keystrokes with the index finger (Fig. 9A), the synchrony of the motion at the MCP joint across fingers decreased as the cluster number increased, the averaged correlation coefficients of MCP motion across fingers decreasing from 0.47 for cluster 1 to 0.15 for cluster 3. The motion at the PIP joints and abduction/adduction across fingers were fairly small relative to
the MCP joint motion for all of the three clusters. This small amplitude of averaged PIP motion is not a
result of variable motion across tone sequences, because the PIP motion was consistent within each
cluster (Fig. 8A). In all three clusters, thumb internal rotation and abduction paralleled each other, with a
time course that differed from cluster to cluster (left panels of Fig. 9A and 9B).

To assess whether fingering could characterize the individual clusters, using data from all
subjects for each cluster, we computed the mean value of the proportion of tone sequences with different
digits used prior to and following the keystroke (Fig. 10). Overall, the individual clusters involved use of
different fingers prior to and/or following the keypress, which confirmed that fingering determined the
joint coordination pattern. For the index finger keystroke, clusters 1 and 3 were mostly characterized by
use of the thumb one stroke before and after the index keypress, respectively. For the middle finger
keystroke, more than 80% of tone sequences in cluster 1 and 2 involved preceding use of the index and
ring finger, respectively. Cluster 3 was characterized by use of either the thumb or the little finger one
stroke before the middle keypress. For the ring finger keystroke, sequences in cluster 2 were mostly
associated with use of the thumb one stroke before the ring keypress, followed by the middle keypress. To
the contrary, around 80% of sequences in cluster 1 involved the keypress with either thumb or little finger
prior to the ring keypress, followed by the keypress with either the thumb, index, or little finger. The
cluster 3 was mostly characterized by use of either index or middle finger prior to the ring keypress. For
the little finger keystroke, cluster 1 and 3 was characterized by a thumb keypress one stroke after and
before, respectively.

Figure 10 inserted here

We also computed the mean value of the proportion of tone sequences with different digits used
two strokes before and after the keystroke. The results showed that the fingering two strokes before and
after the target keystroke failed to characterize the individual clusters, except for cluster 2 of the ring
finger keypress, where 85.9 ± 14.1 % of all tone sequences in this cluster were associated with use of the
index finger two strokes before the ring keystroke.

To quantitatively evaluate the covariation of movements across joints for each of the clusters,
we performed a linear regression analysis. For each cluster and for keystrokes with each of the fingers, we
compared the waveform of the MCP joint velocity at the striking finger to the waveforms of the MCP of
the adjacent fingers and the PIP of all fingers. Figure 11 summarizes the mean gain (left panel) and $r^2$
(right panel) values derived from the analysis across all 5 subjects. Overall, the MCP gain values were
much less than 1, which indicated only partial spillover of motion at the striking finger to other fingers.
The exception was the ring MCP of cluster 1 during the little finger keystroke. The gain value, on average,
did not differ depending on the finger used for the keystroke, which indicated similar lack of spillover
across fingers of the striking finger motion to the adjacent fingers. A comparison across joints revealed
that gain values were larger at the MCP joint of the fingers adjacent to the striking finger as compared to
the other joints. A two-way repeated measures ANOVA revealed a main effect of joint for the index ($F_{(2,8)} = 64.6$), middle ($F_{(2,8)} = 6.5$), ring ($F_{(2,8)} = 11.5$) finger keystrokes ($p<0.05$). This tendency was also
observed in the $r^2$ values, particularly during the middle and ring keystrokes. A two-way repeated
measures ANOVA revealed a main effect of joint for the middle ($F_{(2,8)} = 14.3$) and ring ($F_{(2,8)} = 7.1$) finger
keystrokes ($p<0.05$). For the little finger keystroke, the gain value was relatively large and variable across
subjects, presumably due to the fairly small magnitude of little MCP motion particularly for two of five
subjects.

*Figure 11 inserted here*

A two-way repeated measures ANOVA using joint and cluster as independent variables
revealed that both gain and $r^2$ values differed across clusters for the keystroke of each of the four fingers
($p<0.05$), which confirmed inter-cluster differences in the spill-over of motion at the striking finger to the
adjacent fingers. Overall, the inter-cluster differences were most evident at the finger adjacent to the
striking finger for both gain and $r^2$ values. In addition, the inter-cluster differences in these values tended
to be related to fingering. For the $r^2$ value at the MCP joint, there was a tendency to have a smaller value
at the finger used prior to and/or following to the keypress (see Fig. 10). This was also the case for the
gain value at the MCP joint, except for the index keypress, being characterized by a higher value at the finger used prior to the keypress.

**Similarity of results of cluster analysis across subjects**

To evaluate to what extent the result of the cluster analysis was consistent across subjects, we computed a “correspondence index” by calculating, for each tone sequence, the proportion of subjects who were assigned into each cluster. We then took the value for the cluster with the largest number of subjects, and averaged these values across all tone sequences. The result showed that the correspondence index ranged from 0.88 ± 0.15 (thumb) to 0.78 ± 0.15 (ring, mean ± SD across sequences). Thus, the cluster analysis assigned tone sequences into distinct clusters in a consistent manner across subjects.

We also assessed the similarity of waveforms across subjects for each of the clusters. To this end, we performed a linear regression analysis across joint velocity waveforms for pairs of subjects for each cluster. Table 2 summarizes the average $r^2$ value derived from the analysis across all pairs of subjects. Results showed that the $r^2$ value averaged 0.55, ranging from 0.43 to 0.68. This largely reflected differences in kinematic waveforms across subjects (e.g. PIP joint motion in Fig. 4), because a given sequence tended to be assigned consistently to a given cluster.

*Table 2 inserted here*
Comparison of the results of cluster analysis across composers

Conceivably, the joint coordination pattern may reflect the musical styles of each composer and tone sequences by a particular composer might be categorized into a particular cluster. However, for each of the three composers, tone sequences turned out to be assigned in almost equal proportions into each of the clusters. There was one exception involving the composer Moszkowski and keypresses executed by the thumb and middle finger, where a proportionally larger number of tone sequences were assigned into cluster 2 and 3. Thus our findings do not support the hypothesis that several distinct joint coordination patterns reflected different styles of composition. (Note however that all selections were played legato and therefore our findings may not hold true for pieces played staccato.)

DISCUSSION

The present study aimed to determine whether hand movements during piano playing can be characterized either by coupled or by individuated motions. Our results supported both of these tendencies. For a keystroke with the thumb, we identified two characteristic patterns of finger joint movement coordination associated with distinct thumb movements. However, both of these patterns displayed strongly coupled motions across the 4 fingers at the MCP and PIP joints. For a keystroke with each of the four fingers, by contrast, the movement patterns for different tone sequences were generally segregated into three clusters. The MCP joint motion at the striking finger was fairly consistent across
clusters, but the motion of the non-striking fingers differed, largely depending on the finger used to strike
the preceding or succeeding key. The lack of coupling of the motion at adjacent fingers indicated highly
individuated finger movements during skilled piano playing.

**Coupling of finger movements during thumb keystrokes**

For the thumb keystroke, motions at all 4 fingers were coupled together at the MCP as well as
the PIP joints for both of the two clusters. This type of joint coordination was also evident for PC1, which
was commonly used for all tone sequences. Moderately coupled joint rotations at the fingers is a pattern
also observed in various hand manipulation tasks, such as grasping (Santello et al. 2002; 1998), typing
(Soechting and Flanders 1997), and haptic exploration (Thakur et al. 2008).

By contrast, the pattern of joint rotation at the thumb differed between the two clusters,
particularly in the timing of thumb internal rotation, MCP flexion and abduction relative to the keypress.
We found that the two clusters corresponded to the direction of the thumb-under maneuver. For a
thumb-under movement to the right, a key struck by the finger prior to the thumb keypress is located to
the left of the key subsequently struck by the thumb. This requires large displacement of the thumb
toward the key to be struck, without altering the posture of the hand. This can be achieved by a
preparatory thumb rotation. By contrast, during the thumb-under maneuver to the left, the key struck
previously by a finger is located right of the key to be struck by the thumb. The thumb therefore need not
move a long distance to strike the key, whereas the hand requires a large rotation to position the finger used for the subsequent keypress. Taken together, task constraints of both fingering and location of keys to be struck appeared to determine the timing of thumb rotation. This supposition was confirmed quantitatively by the PI value, reflecting both fingering and key location, which displayed the opposite sign between these two clusters. Furthermore, the PI value was correlated with cluster membership also for tone sequences without a thumb-under maneuver (Fig. 5B), indicating that task constraints regarding fingering and key locations determine joint coordination patterns in the same manner irrespective of the presence or absence of thumb-under.

Independent control of finger movements

In contrast to the coupled motions across fingers in a wide variety of tone sequences involving the thumb keystroke, keypresses executed by each of the fingers were characterized by individuated movements across fingers. While the MCP joint motion at the striking finger was consistently characterized by a tri-phasic pattern (Figs. 6 and 7), the MCP joint motion at other fingers varied considerably across clusters, primarily depending on the finger used for the previous or subsequent keypress (Fig. 9). The lack of consistency of motions at the non-striking fingers was observed even for motions at the middle MCP joint for keys struck with the ring finger (Fig. 7B), an instance in which there is strong coupling in other tasks (Häger-Ross and Schieber 2000; Zatsiorsky et al. 2000).
Previous studies have commonly reported a hierarchy of independence of finger movements, middle and ring fingers eliciting a larger movement spillover than index and little fingers (Häger-Ross and Schieber 2000; Lang and Schieber 2004; Soechting and Flanders 1997). By contrast, the present study displayed more limited evidence for this hierarchy in piano playing. In addition to inconsistent motions at the non-striking fingers relative to the striking finger motion for a keypress with any of fingers, the amount of movement spillover of the striking finger to the adjacent fingers was overall similar irrespective of the finger used for the keystroke (Fig. 10). However, we did observe that the largest amount of spillover was to adjacent, rather than non-adjacent fingers.

The lack of independence of movements across fingers has been considered to originate from anatomical and neural constraints at the hand. For example, extrinsic finger muscles are inserted into multiple digits and various tendons are interconnected (Leijnse 1997; Tubiana 1981; Watson 2006). Peripheral neural coupling across digits also exists in the form of synchronized activity of motor units in different compartments of the multi-tendoned flexors and extensor of the digits (Keen and Fuglevand 2004; Kilbreath and Gandevia 1994; Winges et al. 2008). Furthermore, motor cortical representations of the muscles moving different digits or individual joints overlap to a great extent (Sanes et al. 1995; Schieber and Hibbard 1993). However, some studies have reported weaker synchronization of motor unit activity within a single hand muscle for musicians than for non-musicians (Semmler and Nordstrom 1998;
Semmler et al. 2004) and a less pronounced difference in cortical activity associated with the index and ring fingers for pianists compared to non-musicians (Slobounov et al. 2002). In addition, deliberate practice of individuated finger forces enhanced independent control and concurrently produced changes in cortical activity (Chiang et al. 2004). Thus the plastic changes in neural constraints via extensive practice may ensure relatively independent control of movements across fingers for expert pianists.

**Temporal constraints on multijoint movements**

Individual clusters, being characterized by different patterns of joint coordination, were associated with distinct fingerings as to which fingers were used prior to and following a keypress. Overall, the striking finger moved most independently from the finger used prior to or following the target keypress. This can be related to the present task constraint of not releasing a key before the next key is depressed (i.e., *legato*) (Repp 1995). We observed that the striking motion was initiated and terminated approximately one stroke prior to and following the keypress, respectively. Joint motions responsible for two successive keystrokes therefore overlapped. Hence, the fingers used for the two successive keypresses needed to move independently in order to circumvent inaccuracy of timing and intensity of tone production. The temporal constraint on movements during piano playing but not during other hand tasks such as grasping and typing may result in a more independent control of fingers in the present motor task.
A movement pattern common across various motor tasks is coupled motions at multiple joints, such as in grasping (Mason et al. 2001; Santello et al. 2002; 1998), reaching (Hollerbach and Flash 1982; Soechting and Lacquaniti 1981), wiping (Giszter et al. 1989; Ostry et al. 1991), trunk bending (Alexandrov et al. 1998; Berret et al. 2009), and sitting-up (Cordo and Gurfinkel 2004). A common feature of these tasks is that there is often no explicit or strict temporal constraint on the movement. Similarly, typing with no temporal constraint (Flanders and Soechting 1992) was also characterized mostly by coupled motions across fingers (Soechting and Flanders 1997). By contrast, in piano playing with strong temporal constraints, individual fingers move differently depending on the context of movements so as to accomplish smooth transition of successive motions. An intermediate between these two extremes may be finger-spelling with slight temporal constraints, where the index and middle PIP joints tend to follow a different pattern of coarticulation, involving faster movements, compared to the slower postural changes of the thumb and wrist (Jerde et al. 2003). Taken together, we speculate that temporal constraints on movements would be a crucial factor determining whether motions of multiple degrees of freedom at the motor system are organized synergistically or independently. This may influence pathophysiological differences between writer’s cramp and musician’s focal dystonia (Rosenkranz et al. 2005).
ACKNOWLEDGEMENTS

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DISCLOSURES

The authors declare no conflict of interest.
REFERENCE


Figure 1. Representative music excerpts from Bach (A), Chopin (B), and Moszkowski (C). Numbers below each score indicate fingering (1, 2, 3, 4, and 5 corresponds to the thumb, index, middle, ring, and little finger, respectively.).

Figure 2. Representative tone sequences of five successive strokes having a keypress with each digit at the center of the sequence. There were 64, 64, 49, 56, and 51 sequences centered on the keypress with thumb, index, middle, ring and little finger, respectively. For the thumb sequences there were 8 with thumb-under and hand moving left-to-right, 7 with thumb-under and hand moving right-to-left, and 49 without thumb-under.

Figure 3. The average angular velocity waveforms across all tone sequences having a thumb keypress at the center of the sequence, and the waveforms for the first three PCs in one subject (subject 4). The PCs were computed using all 64 thumb keypress sequences (with and without thumb-under). One inter-keystroke interval corresponds to 100 normalized time units (about 124.5 ± 2.0 ms). Time zero indicates the moment of the thumb keypress. A positive and negative value indicates flexion/abduction/internal-rotation and extension/adduction/external-rotation, respectively. I-M, M-R, and
R-L indicates the index-middle, middle-ring, and ring-little abduction/adduction, respectively. An arrow indicates the moment of each of five keypresses (= when a key started to descend).

Figure 4. Results of the principal component analysis for all tone sequences with the thumb keypress in one subject (subject 4). A: Weighting coefficients of the first four PCs for each sequence. Black and white bars in represent different clusters. Note that tone sequences with the thumb-under (TU) showed opposite signs of WC2 depending on the direction of movement. B: A scatter plot of the weighting coefficients of the first three PCs. Black and white dots represent different clusters. C: Variances accounted for by individual PCs.

Figure 5. For two representative subjects (subject 3 at the top, and subject 4 at the bottom), averaged angular velocity waveforms were reconstructed using the first four PCs (see Figure 2). These reconstructions are shown separately for the sequences belonging to cluster 1 (above) and cluster 2 (below).

Figure 6. Combined results from all subjects summarize the similarities and differences between the two clusters. A: The mean value of the proportion of tone sequences without thumb-under (light gray), with
the left-to-right thumb-under (LR TU, medium gray), and with right-to-left thumb-under (RL TU, dark gray). **: The mean value of the postural index (PI). C, D: The mean value of the weighting coefficients of the first two PCs. An error bar indicates one SE (n=5). **: p<0.01

Figure 7. The average joint velocity waveforms across all tone sequences having a keypress with the index, middle, ring or little fingers at the center of the sequence in one subject (subject 2).

Figure 8. For all tone sequences centered on the index (top) and ring (bottom) keystrokes, the individual joint velocity waveforms at the MCP (above) and PIP (below) joints are superimposed for the index, middle, ring and little fingers (columns). All data are from the same subject as in Fig 6 (subject 2). Lines in different colors represent different clusters.

Figure 9. The average joint velocity waveforms for each of the three clusters (rows), for sequences centered on the index (A) and ring (B) keystrokes. All data are from subject 5.

Figure 10. Combined results from all subjects summarize the similarities and differences between the three clusters. The mean value of the proportion of tone sequences with different digits (gray scale) used
prior to (left column) and following (right column) the keystroke with the index, middle, ring or little
fingers (top to bottom rows) is shown for each of the three clusters.

Figure 11. Combined results from all subjects summarize the differences in covariation of joint
movements across the three clusters. The average of gain (left column) and $r^2$ values (right column)
derived from a line regression analysis between the MCP joint of the striking finger and the remaining
MCP and PIP joints of fingers (x-axis). The data points are averages across subjects for each of three
clusters during the keystroke with the index, middle, ring or little fingers. A circle, triangle, and squared
symbol represents cluster 1, 2, and 3, respectively. An error bar indicates one SE (n=5). *: $p<0.05$, **: $p<0.01$ with Newman-Keuls post-hoc test.
Cluster 1 (deg/s)  
Cluster 2 (deg/s)  

Subject 3  
Subject 4
one previous stroke

one subsequent stroke

index keystroke (%)

middle keystroke (%)

ring keystroke (%)

little keystroke (%)

cluster

cluster
Table 1. Average of variance accounted for by the first four PCs across subjects for the keystroke by each of five digits.

<table>
<thead>
<tr>
<th></th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
<th>PC4</th>
<th>PC1+2+3+4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thumb</td>
<td>36.7 (5.4)</td>
<td>18.2 (4.1)</td>
<td>8.5 (0.5)</td>
<td>6.7 (0.8)</td>
<td>70.1 (4.1)</td>
</tr>
<tr>
<td>Index</td>
<td>28.9 (3.2)</td>
<td>18.3 (2.1)</td>
<td>12.4 (1.5)</td>
<td>7.2 (1.1)</td>
<td>66.7 (2.1)</td>
</tr>
<tr>
<td>Middle</td>
<td>29.1 (6.1)</td>
<td>16.0 (2.2)</td>
<td>12.5 (1.3)</td>
<td>8.0 (1.0)</td>
<td>65.6 (3.8)</td>
</tr>
<tr>
<td>Ring</td>
<td>32.7 (3.8)</td>
<td>13.5 (0.8)</td>
<td>10.7 (0.9)</td>
<td>8.2 (0.4)</td>
<td>65.2 (3.7)</td>
</tr>
<tr>
<td>Little</td>
<td>24.9 (3.3)</td>
<td>16.5 (2.0)</td>
<td>11.9 (1.4)</td>
<td>8.4 (1.5)</td>
<td>61.8 (4.7)</td>
</tr>
</tbody>
</table>

A number in parenthesis indicates SD across five subjects.
Table 2. The mean $r^2$ value of joint velocity waveforms across any pair of five subjects for each cluster.

<table>
<thead>
<tr>
<th></th>
<th>Cluster 1</th>
<th>Cluster 2</th>
<th>Cluster 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thumb</td>
<td>0.56 (0.09)</td>
<td>0.68 (0.08)</td>
<td></td>
</tr>
<tr>
<td>Index</td>
<td>0.60 (0.09)</td>
<td>0.65 (0.08)</td>
<td>0.56 (0.07)</td>
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<tr>
<td>Middle</td>
<td>0.57 (0.10)</td>
<td>0.57 (0.10)</td>
<td>0.62 (0.08)</td>
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<tr>
<td>Ring</td>
<td>0.48 (0.16)</td>
<td>0.61 (0.10)</td>
<td>0.43 (0.13)</td>
</tr>
<tr>
<td>Little</td>
<td>0.43 (0.10)</td>
<td>0.50 (0.26)</td>
<td>0.50 (0.18)</td>
</tr>
</tbody>
</table>

A number in parenthesis indicates SD across five subjects. The value is the average across all joints.