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RESEARCH ARTICLE

The statistics of natural hand movements

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Abstract Humans constantly use their hands to interact with the environment and they engage spontaneously in a wide variety of manual activities during everyday life. In contrast, laboratory-based studies of hand function have used a limited range of predefined tasks. The natural movements made by the hand during everyday life have thus received little attention. Here, we developed a portable recording device that can be worn by subjects to track movements of their right hand as they go about their daily routine outside of a laboratory setting. We analyse the kinematic data using various statistical methods. Principal component analysis of the joint angular velocities showed that the first two components were highly conserved across subjects, explained 60% of the variance and were qualitatively similar to those reported in previous studies of reach-to-grasp movements. To examine the independence of the digits, we developed a measure based on the degree to which the movements of each digit could be linearly predicted from the movements of the other four digits. Our independence measure was highly correlated with results from previous studies of the hand, including the estimated size of the digit representations in primary motor cortex and other laboratory measures of digit individuation. Specifically, the thumb was found to be the most independent of the digits and the index finger was the most independent of the fingers. These results support and extend laboratory-based studies of the human hand.

Keywords Human hand · Digit independence · Dimensionality of hand movements · Movement statistics

Introduction

One important characterization of the human hand is the number of degrees of freedom (DOF) spanned by its movements. This defines the dimensionality of the control problem solved by the motor system. Anatomically, the five digits of the hand comprise a total of 15 joints, which afford approximately 20 DOFs (Stockwell 1981; Jones 1997). However, the extent to which each of these DOFs is independently controlled during movement is unknown and has been the subject of a number of laboratory-based studies (reviewed by Jones and Lederman 2006). It is known, for example, that the mechanical architecture of the hand places constraints on the independent control of the digits (von Schroeder and Botte 1993; Lang and Schieber 2004). The neural and neuromuscular architecture of the hand appears also to limit the degree of independent control (Kilbreath and Gandevia 1994; Lemon 1997; Reilly and Schieber 2003). Moreover, it is thought that the motor system may employ synergies to reduce the dimensionality of the hand and thus simplify the control problem (reviewed by Schieber and Santello 2004; see also Tresch et al. 2006). The existence of such synergies has been characterized by applying statistical techniques, such as principal component analysis (PCA) and non-negative matrix factorization

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(NMF), to kinematic (Santello et al. 1998; Mason et al. 2001; Santello et al. 2002; Todorov and Ghahramani 2004) and EMG (Weiss and Flanders 2004) data collected from human subjects performing laboratory-based tasks (see also Brochier et al. 2004; d'Avella et al. 2006). In other studies the degree to which humans are capable of making individuated movements of each digit has been examined (Häger-Ross and Schieber 2000). The general conclusion of these studies is that the effective dimensionality of the human hand is much less than the 20 DOFs, which are theoretically available for movement.

Many studies have analysed reach-to-grasp movements and characterized hand kinematics (Santello et al. 1998; Santello and Soechting 1998; Mason et al. 2001; Santello et al. 2002). These studies report high correlations between the angles of the major joints of the fingers. For example, PCA of joint angles reveals that the first two to three components explained the vast majority of the variance in hand posture. These results suggest dimensionality reduction and may be evidence for the existence of motor synergies in the control of the hand. This idea is strengthened by the finding that it is difficult for human subjects to move one digit without some degree of involuntary movement at one or more of the other digits. In a kinematic study of digit independence Häger-Ross and Schieber (2000) developed an Individuation Index to quantify the ability of each digit to move without associated movements of the other digits. The thumb scored highest on the individuation scale, followed closely by the index finger, with the little finger third in the ranking, followed by the middle finger and finally the ring finger with the lowest score. Digit independence has also been examined using force production tasks with similar findings. Zatsiorsky et al. (1998) asked subjects to produce force at a single finger and examined the involuntary production of forces (enslaving) at the other fingers. They report large enslaving effects for all fingers indicating an inability of subjects to individuate force production. The effects were always largest for the immediate neighbours of the task finger with more distant fingers exhibiting smaller enslaving effects. Reilly and Hammond (2000) also measured force production by digits when subjects where instructed to produce force at a single digit and similarly reported involuntary forces at non-instructed digits. These were smallest when the instructed digit was the thumb, increasing, respectively, for the index, middle and little fingers and were largest for the ring finger.

The above conclusions about the reduced dimensionality of the hand and limited individuation of the digits are based on data collected during laboratory-based experiments using fixed tasks. These necessarily impose constraints on the variety of hand movements permitted. Here, we address this issue by analysing a natural movement dataset collected from the right hand of subjects by way of a wearable motion tracking system. This allowed our subjects to engage spontaneously in normal everyday tasks outside of a laboratory setting. Just as many properties of sensory systems can be understood in terms of the statistics of their natural stimuli (Ruderman and Bialek 1994; Olshausen and Field 1996; Schwartz et al. 2003; Körding et al. 2004), we suggest that statistical analyses of the range of natural movements made during everyday life can contribute to our understanding of the motor system.

Methods

Subjects

Six healthy male subjects, aged 31–43 gave informed consent and participated in this study. Three of the subjects were authors and three were volunteers who were naive to the purpose of the experiment. No qualitative differences were observed between these groups. The experimental protocol was approved by the local ethics committee.

Data acquisition

Movements of the right hand were measured using resistive sensors embedded in a cloth glove (CyberGlove, Virtual Technologies, Palo Alto, CA, USA). The sensors were associated with 19 DOF of the hand (Fig. 1a) and consisted of the metacarpal-phalangeal (MCP), proximal interphalangeal (PIP) and distal interphalangeal (DIP) joint angles for the four fingers (Index: I, Middle: M, Ring: R, Little: L), the three relative abduction angles between the four fingers (I/M-ABD, M/R-ABD, R/L-ABD), the carpo-metacarpal (T-CMC), metacarpal-phalangeal (T-MCP) and interphalangeal (T-IP) joint angles for the thumb (T) and the abduction angle (T-ABD) between the thumb and the palm of the hand. Sensors were sampled continuously at 84 Hz at a resolution of 8 bits per sensor. This gave an effective sensor resolution between 0.3° and 0.9° depending on the sensor and calibration for each subject (mean ± SD over all sensors and all subjects 0.6° ± 0.2°). The palmer surface of the CyberGlove is a flexible fishnet material permitting free movement and a degree of cutaneous sensation, which would be impaired by a traditional cloth glove. Although wearing a glove may alter tactile feedback, on questioning, subjects did not complain of any specific restriction of their movements.

Subjects wore a small backpack that weighed approximately 5 kg and contained a laptop computer, the digitizing control unit for the glove, a 12-V battery pack and DC power regulator. The backpack was a standard off-the-shelf item, which was unmodified and secured to the subject by its shoulder straps. The glove was connected by a cable to

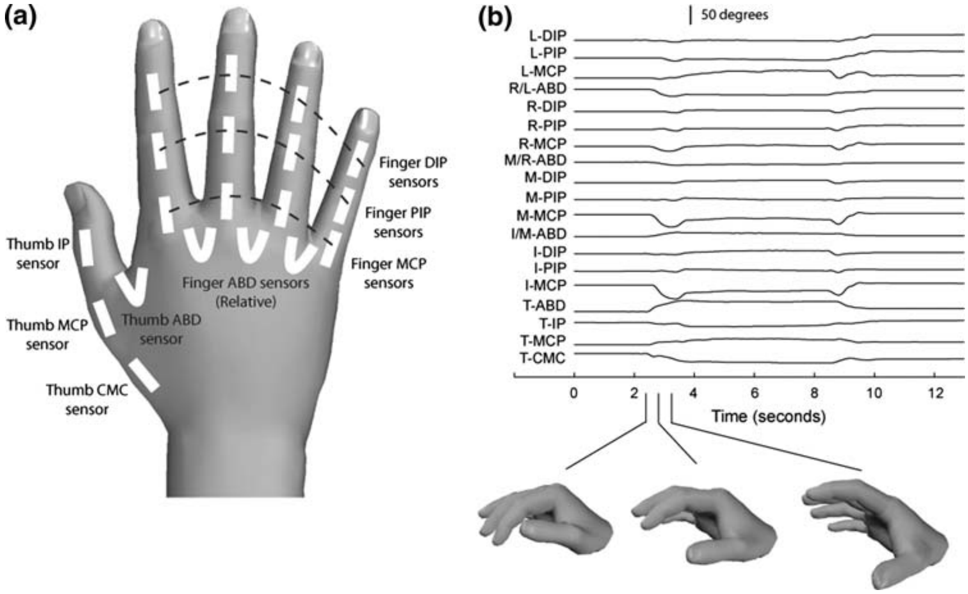

Fig. 1 CyberGlove sensor placement and example joint angle traces. **a** Placement of sensors on the CyberGlove. *CMC* carpal-metacarpal joint, *MCP* metacarpal-phalangeal joint, *PIP* proximal inter-phalangeal joint, *DIP* distal inter-phalangeal joint, *IP* inter-phalangeal joint, *ABD* abduction joint. **b** Example traces for the 19 measured joint angles with three frames taken from an animation showing the hand opening to grasp a glass. Digit abbreviation as follows: *T* thumb, *I* index, *M* middle, *R* ring, *L* little. Sensor abbreviations as above

the digitizing controller in the backpack, which was read via the serial interface on the laptop. The glove's cable was secured to the forearm and upper arm using adjustable Velcro straps. The backpack contained all the hardware required for the data acquisition and allowed the subject full mobility. Subjects wore the backpack and glove for one or two recording sessions, which (depending on battery life) could last up to 2 h. A flashing LED on the base of the glove indicated that the recording session was in progress. Subjects were instructed to go about their normal routine and return to the lab when the LED stopped flashing. The only restriction was to avoid doing anything, which might soil the glove or get it wet.

Calibration

The glove was calibrated for each subject using a three-step procedure. In step one, a simple two-point calibration was performed for each joint using a mechanical splint. This was performed only once for each subject and provided an approximate linear calibration between sensor output and joint angle. In step two, which was performed before every recording session, the linear calibration was further refined using an online visualization system. This used a realistic computer-generated OpenGL rendering to create an image of a virtual human hand. The virtual hand was displayed on a stereoscopic 3D graphics system and by using a semi-silvered mirror, the image was overlaid on the subject's own hand. The virtual hand was animated in real-time by data from the glove. The calibration for each sensor was manually adjusted until the movements of the virtual hand closely matched those of subject's hand. In step three, a zero point for all sensors was set using a standard posture as follows. Subjects were instructed to place their hand palm-down against a flat surface with the four fingers parallel and the thumb aligned against the side of the palm. A reading was then taken from the glove and this served as the zero point for joint angles in the subsequent recording session. The visualization system used in step two allowed the calibration of the glove to be verified. An offline figure animation package (Poser, Curious Labs Inc., Santa Cruz, CA, USA) was used to visualize and illustrate hand postures.

Data analysis

Joint angle data for the 19 sensors and a time-stamp for each sample were stored to disk for offline analysis using MatLab (Release 14, The MathWorks, Natick, MA, USA). The quantization of the 8-bit sensor data was smoothed using a linear phase FIR filter designed in MatLab using the Generalized Remez FIR filter design function. The filter length was 151 samples and its frequency response yielded zero attenuation at or below 4.2 Hz and 90 dB attenuation at or above 6.4 Hz. Angular velocities were calculated from the first difference of the filtered joint angle data divided by the time step. Datasets from the multiple recording sessions for each subject were concatenated and the analyses were performed on the complete datasets for each subject. Subject means are reported in all cases. Basic statistics for individual joints were calculated for both joint angles and angular velocities (we use the term joint to refer to a single DOF). During the analysis of joint angles we found occasional outliers in the data, which we attributed to sensor deformations caused by contact of the sensor-surface of the glove with objects in the environment. Such outliers were very rare and were removed from the statistical analysis of joint angles by excluding values outside the 99.8% percentiles.

The dimensionality of hand movements was examined by means of a PCA of the angular velocities. Angular velocities were also used to calculate correlation coefficients between the flexion/extension joints (MCP, PIP and DIP) of the four fingers. Whereas previous studies have performed such analyses on angular positions, angular velocities were chosen in this case because they are more closely related to the motor commands driving movement (Todorov and Ghahramani 2004).

Inspired by previous studies, which have characterized the degree of independence of the digits (Kilbreath and Gandevia 1994; Häger-Ross and Schieber 2000) we developed new measures of digit independence based on the linear predictability of the movements of each digit. A velocity matrix was created for each digit using the instantaneous angular velocities calculated from the filtered joint angle data as described above. The matrix for each digit consisted of a time series (rows) of angular velocities (columns) for the four joints of each digit. The columns of the velocity matrix for the thumb came directly from the angular velocities derived from its four sensors. For the fingers, three columns of the velocity matrix came directly from the angular velocities derived from the three flexion/extension sensors. It was necessary to estimate the fourth (abduction) column of the velocity matrix from angular velocities derived from the three sensors, which measured the relative abduction angle between the four fingers (see Fig. 1a). Half the angular velocity associated with each sensor was assigned equally to the two adjacent fingers. This method would be expected to slightly under-estimate measures of finger individuation. However, these effects will be minimal due to the much greater contribution from the flexion/extension joints relative to abduction.

The velocity matrices were used to calculate three measures to quantify the movements of the digits. The first measure quantified the total amount of movement associated with each digit and was calculated by taking the unsigned sum of the four elements in the velocity matrix across time and across joints. The resulting value expressed the total angular path length for each digit and was normalized across the five digits.

The second measure quantified digit independence. We used linear regression to fit each component of the velocity matrix of a given digit as a function of the velocity matrices of the other four digits collectively. We then calculated the percentage of the digit's movements that were unexplained by this linear fit. More specifically, we calculated the ratio of the variance of the residual of the linear reconstruction to the total variance for that digit. This yielded a single value expressed as a percentage for each digit of the hand. Because this measure was designed to quantify the independence of each digit's movements, it was expressed as percent unexplained variance. As such, a value of 0% would indicate that the movements of a particular digit could be completely predicted by linear reconstruction using the movements of the other four digits. Conversely, a value of 100% would indicate that none of the movements of a particular digit could be predicted from the other four digits.

The third measure quantified the degree of coupling between digit pairs. We used linear regression to fit the velocity matrix of a given digit as a function of the velocity matrices of each of the other four digits individually. It thus yielded four values for each digit (one value for each pairing of the digit with the other four digits) to give a total of 20 values for the hand. These values were expressed as the percentage of total variance of a digit's velocity matrix that could be explained by a linear reconstruction based on its paired regressions with each of the other four digits. Because this measure was designed to quantify coupling between the digits, it was expressed as percent explained variance. As such, a value of 100% for a particular digit pairing would indicate that the movements of one digit could be completely predicted by linear reconstruction using the movements of the other digit. Conversely, a value of 0% would indicate that none of the movements of the digit could be predicted from the movements of the other.

A final analysis was performed in which we determined the percentage time that each digit was moving. A cut-off velocity was chosen (20 deg/s) to convert the velocity data to binary flags that indicated the periods of movement for each digit. This binary data was then used to determine the total time that each digit was moving as well as the percentage of those movements that occurred while other digits were stationary. We called this measure the percent exclusive movements because it indicated the percentage of movements that were exclusive to each digit. We also determined movement time percentages for various combinations of the digits, including movements of the fingers both with and without accompanying movements of the thumb.

Results

We obtained datasets of spontaneous everyday hand movements from six subjects during recording sessions, which lasted an average of 93 ± 7 min each (range 84–108 min). One subject completed a single recording session and the remaining five subjects completed two sessions (on different days). A total of 16 h 57 min of data were collected (range 86–206 min per subject). Each dataset represented the postural configuration of the digits of the hand as a function of time and consisted of 19 joint angles sampled continuously at 84 Hz (see "Methods" and Fig. 1a). As an example, we show the angular trajectories obtained while a subject was reaching for a glass of water (Fig. 1b). The figure shows the angular trajectories (top) for the 19 joints and 3 static hand postures (bottom) from the sequence as the hand was opening (time indicated by lines). Post-experimental questioning of subjects showed that they had engaged in a wide variety of tasks both indoors and outdoors including shopping, cycling, eating, drinking, typing, food preparation and reading.

Basic statistics

As a first step in the analysis we examined the basic statistics of the dataset (Table 1, Fig. 2). The hand posture representing the mean joint angle is shown in Fig. 2a. The skew of the angle distributions indicates whether a particular joint is more often extended (negative skew) or more often flexed (positive skew). It varied for each joint (see Table 1). Generally the distributions of angles for the PIP and DIP joints of the fingers were positively skewed as was the distribution of angles for the MCP joint of the little finger (0.8). The distributions of abduction angles between the fingers were also positively skewed. The distribution of angles for the IP joint of the thumb was negatively skewed (−1.0). For the remaining joints, the angular distributions were not greatly skewed. We further quantified the angles and angular velocities using frequency histograms (shown for the index finger in Fig. 2b and c). Note that the percent time for the velocity distributions in Fig. 2c is on a log scale and indicates that the hand spends a considerable proportion of the time not moving. We also calculated the percentage time that any joint was moving faster than a specific angular speed (Fig. 2d). For approximately 50% of the time the angular velocity of all joints was less than 10 deg/s. This corresponds to a very slow movement and indicates that the hand was essentially at rest for approximately half the time. In addition, it was rare to see angular velocity exceed 100 deg/s.

Principal component analysis

Our dataset potentially spans a 19-dimensional space. However, previous studies have suggested that hand movements occupy fewer dimensions than the theoretical maximum. To estimate the dimensionality of the hand movements in our dataset we performed a PCA on joint angular velocities. The first few principal components (PC) of this PCA explained much of the variance (Fig. 3a). For example, the first two PCs accounted for more than half of the variance (60.2 ± 4.1%) and the first ten PCs collectively explained almost all of the variance (93.5 ± 1.1%). Mean correlations between subject pairs for the first two PCs were $r = 0.89 \pm 0.09$ for PC 1 and $r = 0.96 \pm 0.03$ for PC 2 showing that they were well conserved across subjects. The first PC explained 40.5 ± 5.6% of the variance and reflected a coordinated extension (opening) and flexion (closing) of the MCP, PIP and DIP joints of the four fingers. The second PC explained an additional 19.7 ± 4.1% of the variance and also involved the flexion/extension joints of the four fingers. Figure 3b shows how these first two PCs interact to modulate hand posture. The central panel represents the mean hand posture and the edge panels represent the mean hand posture ± one standard deviation weighted for each joint using the coefficients from the first (horizontal axis) and second (vertical axis) PC. As can be seen the first two PCs combine to produce a large range of hand postures. Interestingly, the thumb does not feature prominently in the first two PCs. However, a third PC was well conserved for four of the six subjects (mean correlation between these four subject pairs was $r = 0.88 \pm 0.03$) and explained a further 6.8 ± 1.0% of the variance. The joints of the thumb were prominent in this third PC whereas the joints of the fingers contributed very little. A subject-by-subject analysis of the first eight PCs revealed eight additional components, which followed the pattern of large contributions from the joints of the thumb in conjunction with small contributions from the fingers.

Table 1 Basic statistics of joint angles (degrees) calculated for all data and all subjects

Joint	Mean	SD	Min	Max	Range	Skewness
T-CMC	32	11	−6	64	70	0.3
T-MCP	4	8	−22	33	55	0
T-IP	5	12	−43	36	80	−1
T-ABD	32	10	−4	57	61	0.3
I-MCP	32	16	−25	78	103	−0.1
I-PIP	34	13	−1	84	84	1
I-DIP	15	10	−23	59	82	1.3
I/M-ABD	8	5	−3	32	35	1.3
M-MCP	34	17	−20	79	99	−0.1
M-PIP	38	14	2	87	85	0.7
M-DIP	16	12	−8	70	77	1.3
M/R-ABD	5	4	−5	24	29	1.2
R-MCP	21	15	−18	66	84	0.4
R-PIP	40	16	3	96	93	0.8
R-DIP	12	10	−10	55	65	1.3
R/L-ABD	9	6	−5	37	42	1.1
L-MCP	19	20	−25	80	105	0.8
L-PIP	38	16	−3	92	95	0.6
L-DIP	20	12	−6	68	74	1.2

See “Methods” for joint abbreviations

An additional PCA was performed using joint angles for comparison with the PCs obtained above using angular velocities. The first two PCs obtained from joint angles versus angular velocities were remarkably similar (Table 2) with mean within subject correlations of $r = 0.89 \pm 0.12$ and $r = 0.92 \pm 0.05$ for PC1 and PC2, respectively. The higher order PCs, however, were much less strongly correlated (typical r values between 0.4 and 0.5).

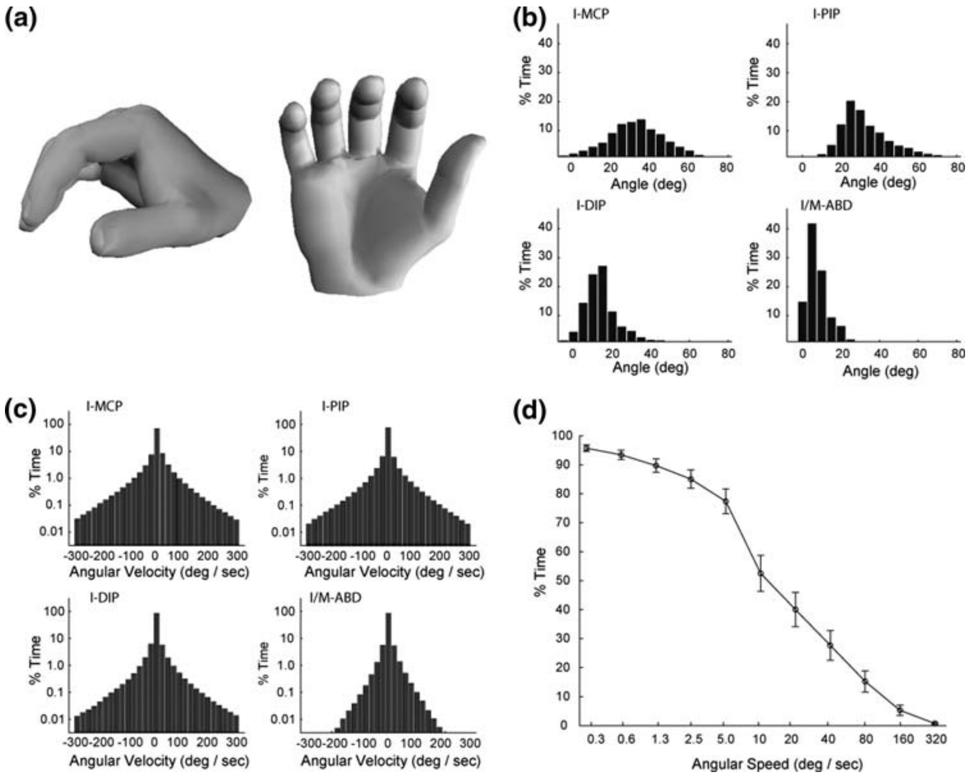

Fig. 2 Basic statistics across all subjects. **a** Two views of the mean hand posture. **b** Histogram of angular data for joints of the index finger. **c** Histogram of angular velocity data for joints of the index finger. **d** Percent time for which the angular speed of any joint is less than or equal to a particular value

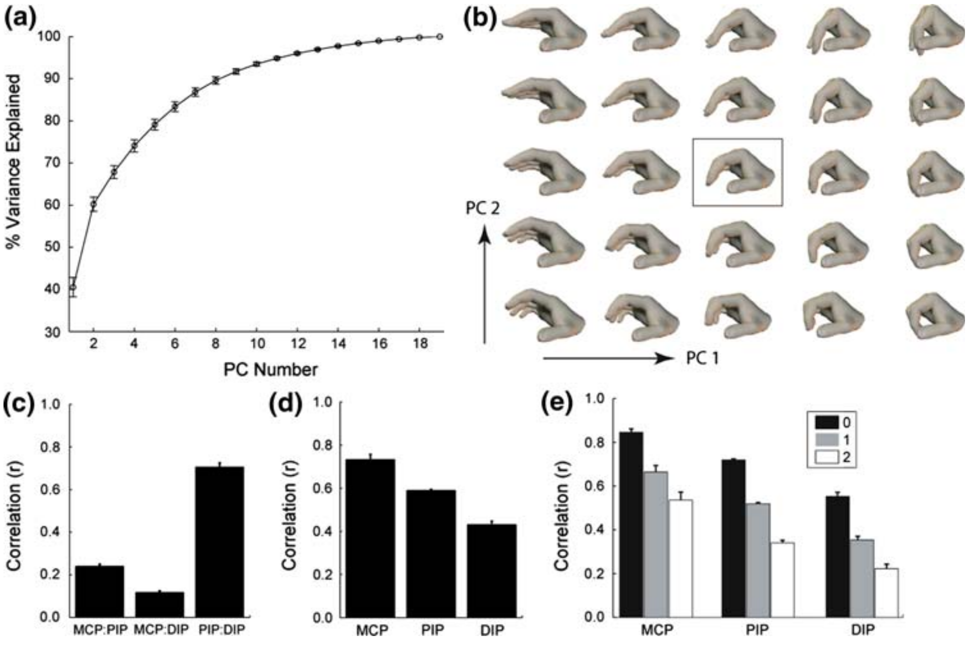

Fig. 3 Principal component analysis (*PCA*) and analysis of correlations. **a** Cumulative variance explained by principal components (*PC*) from a PCA of angular velocities (subject mean and SE). **b** Interaction of the first two principal components. The *boxed centre panel* represents the mean posture over all subjects. The *edge panels* represent the mean posture ± one standard deviation weighted for each joint using the coefficients from the first two principal components (PC1 on horizontal axis and PC2 on vertical axis). **c** Correlations for heterogeneous pairs of the flexion/extension joints within each of the four fingers (subject mean and SE). **d** Correlations for homologous pairs of the flexion/extension joints across the four fingers (subject mean and SE). **e** Correlations for homologous joints for progressively more distant pairs of fingers (subject mean and SE). *Black bars* indicate all pairings of immediate neighbours (distance = 0). *Grey bars* indicate all pairings one finger removed (distance = 1). *White bars* indicate the pairing two fingers removed (distance = 2). *MCP* metacarpal-phalangeal joint, *PIP* proximal inter-phalangeal joint, *DIP* distal inter-phalangeal joint

Table 2 Coefficients for the first and second principal components from PCA of angular positions and angular velocities (subject mean ± SD)

Joint	Angular position		Angular velocity	
	PC1	PC2	PC1	PC2
T-CMC	−0.08 ± 0.08	−0.04 ± 0.16	−0.04 ± 0.05	0.01 ± 0.02
T-MCP	−0.06 ± 0.04	−0.09 ± 0.06	−0.08 ± 0.03	−0.03 ± 0.02
T-IP	−0.03 ± 0.08	0.09 ± 0.14	−0.06 ± 0.04	0.03 ± 0.06
T-ABD	0.08 ± 0.05	−0.02 ± 0.15	0.04 ± 0.03	−0.01 ± 0.03
I-MCP	0.26 ± 0.13	0.30 ± 0.05	0.38 ± 0.10	0.29 ± 0.09
I-PIP	0.21 ± 0.05	−0.11 ± 0.10	0.21 ± 0.05	−0.11 ± 0.06
I-DIP	0.15 ± 0.05	−0.07 ± 0.07	0.12 ± 0.03	−0.08 ± 0.04
I/M-ABD	0.01 ± 0.04	−0.05 ± 0.05	−0.04 ± 0.02	−0.05 ± 0.02
M-MCP	0.32 ± 0.12	0.39 ± 0.06	0.40 ± 0.09	0.41 ± 0.10
M-PIP	0.28 ± 0.09	−0.29 ± 0.06	0.28 ± 0.08	−0.31 ± 0.06
M-DIP	0.22 ± 0.06	−0.24 ± 0.09	0.19 ± 0.06	−0.30 ± 0.07
I/M-ABD	0.01 ± 0.04	−0.05 ± 0.05	−0.04 ± 0.02	−0.05 ± 0.02
R-MCP	0.29 ± 0.07	0.31 ± 0.11	0.30 ± 0.07	0.31 ± 0.07
R-PIP	0.33 ± 0.11	−0.28 ± 0.06	0.32 ± 0.09	−0.33 ± 0.07
R-DIP	0.16 ± 0.06	−0.21 ± 0.06	0.14 ± 0.05	−0.24 ± 0.07
R/L-ABD	0.03 ± 0.02	0.07 ± 0.09	0.05 ± 0.02	0.04 ± 0.03
L-MCP	0.38 ± 0.09	0.31 ± 0.21	0.32 ± 0.07	0.27 ± 0.08
L-PIP	0.31 ± 0.14	−0.26 ± 0.10	0.30 ± 0.09	−0.30 ± 0.06
L-DIP	0.24 ± 0.10	−0.18 ± 0.08	0.20 ± 0.05	−0.23 ± 0.08

See "Methods" for joint abbreviations

Comparison with previous studies

A number of previous studies have analysed hand movement datasets collected in a laboratory setting. An important question arising from the current study is whether there are differences between the statistics of hand movements made in the laboratory and those made during everyday life. For example, Santello et al. (1998, 2002) performed a PCA on joint angles of the hand collected during a reach-to-grasp task. They used a version of the CyberGlove, which did not include the most distal finger joint sensors (DIP). To directly compare our dataset with this previous study, we performed a PCA on joint angles and omitted the finger DIP joints. In this analysis, the first two PCs from our dataset accounted for 70% of the variance, compared to 74% in the previous study. These results indicate that, at least with regards to PCA of joint angles, the hand movements made during a laboratory reach-to-grasp task are representative of the movements made during everyday life.

Correlations between joints of the fingers

To understand the dependencies between the different joints of the fingers we calculated correlation coefficients between the angular velocities of the three flexion/extension joints (MCP, PIP, DIP). Correlations for heterogeneous joint pairs of the fingers (Fig. 3c) were strong between the PIP and DIP joints and weak between the MCP and PIP joins and MCP and DIP joints. Correlations for homogenous joint pairs of the fingers (Fig. 3d) were highest between the MCP joints and decreased progressively for the more distal PIP and DIP joints. Between-finger correlations were highest for immediately neighbouring fingers, falling off for progressively more distant fingers (Fig. 3e). These patterns of correlations suggest a topographic scaling of correlations, with strong correlations between proximal joints versus distal joints and also between immediately neighbouring fingers versus more distant fingers.

Measures of digit independence

The PCA analysis can estimate the dimensionality of the hand's movements but does not provide a measure of the complexity or independence of each digit's movement. To estimate the independence of the digits, we developed three measures based on angular velocity. The first measure was calculated as the total angular path length for each digit (normalized across the five digits) and was designed to quantify the total amount of movement. According to this measure each digit was associated with approximately the same amount of movement (Fig. 4a). However, this result does not capture correlations between the digits, which we addressed by developing a further two measures.

Our second measure was based on the linear predictability of digit angular velocities and was designed to estimate digit independence. Previous studies have shown that in

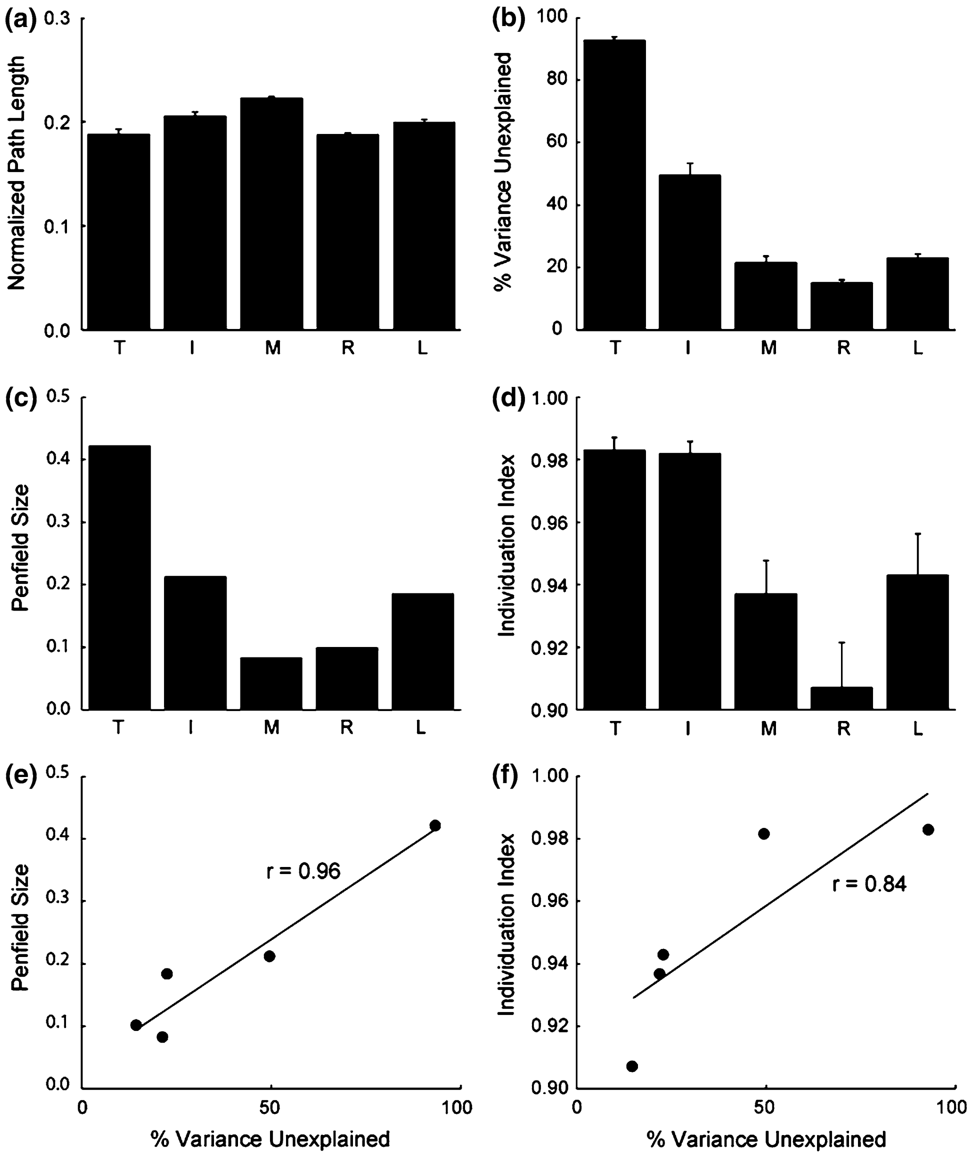

Fig. 4 Analysis of linear predictability of the digits. **a** Total angular path length for each digit normalized across the five digits (subject mean and SE). **b** Percent variance unexplained for each digit after a linear reconstruction of the angular velocities based on all the other digits (subject mean and SE). **c** Penfield Size (data re-plotted from Penfield and Broldrey 1937). **d** Individuation Index (subject mean and SE of data re-plotted from Häger-Ross and Schieber 2000). **e** Correlation between percent variance unexplained (**b**) and Penfield Size (**c**). **f** Correlation between percent variance unexplained (**b**) and Individuation Index (**d**). *T* thumb, *I* index, *M* middle, *R* ring, *L* little

humans, digits such as the thumb and index finger are moved relatively independently, whereas other digits such as the middle and ring fingers are most often moved together with the other digits (Kilbreath and Gandevia 1994; Häger-Ross and Schieber 2000). In terms of neural coding, the amount of information needed to exclusively control the movement of each digit would be expected to vary depending on the degree to which its movements are related to the other digits. Figure 4b shows our measure of digit independence. It is expressed as the percent variance that was unexplained in a linear reconstruction based on the movements of the other four digits. This measure varies across the digits, with the largest amount of unexplained variance associated with the thumb, followed by the index finger, then the little and middle fingers, and was smallest for the ring finger. This pattern of digit independence was correlated with several previous studies (Fig. 4c, d). The Penfield Size, which is the number of cortical sites encoding movement for each digit from the classic study of Penfield (Penfield and Broldrey 1937), is shown in Fig. 4c. It is highly correlated with our digit independence measure ($r = 0.96$, Fig. 4e). The Individuation Index, which is a measure of the ability of human subjects to make individuated movements of each digit, from a study by Häger-Ross and Schieber (2000), is shown in Fig. 4d. Similarly, this measure is highly correlated with our first linear predictability measure ($r = 0.84$, Fig. 4f). The patterns of digit independence in everyday life thus correlate well with laboratory-based measures and the size of the digit representations in the motor system.

Our third measure was also based on the linear predictability of digit angular velocities. It was designed to quantify coupling between pairs of digits (Fig. 5). This measure is expressed as the percent variance that was explained in a linear reconstruction based on pairing the digit with each of

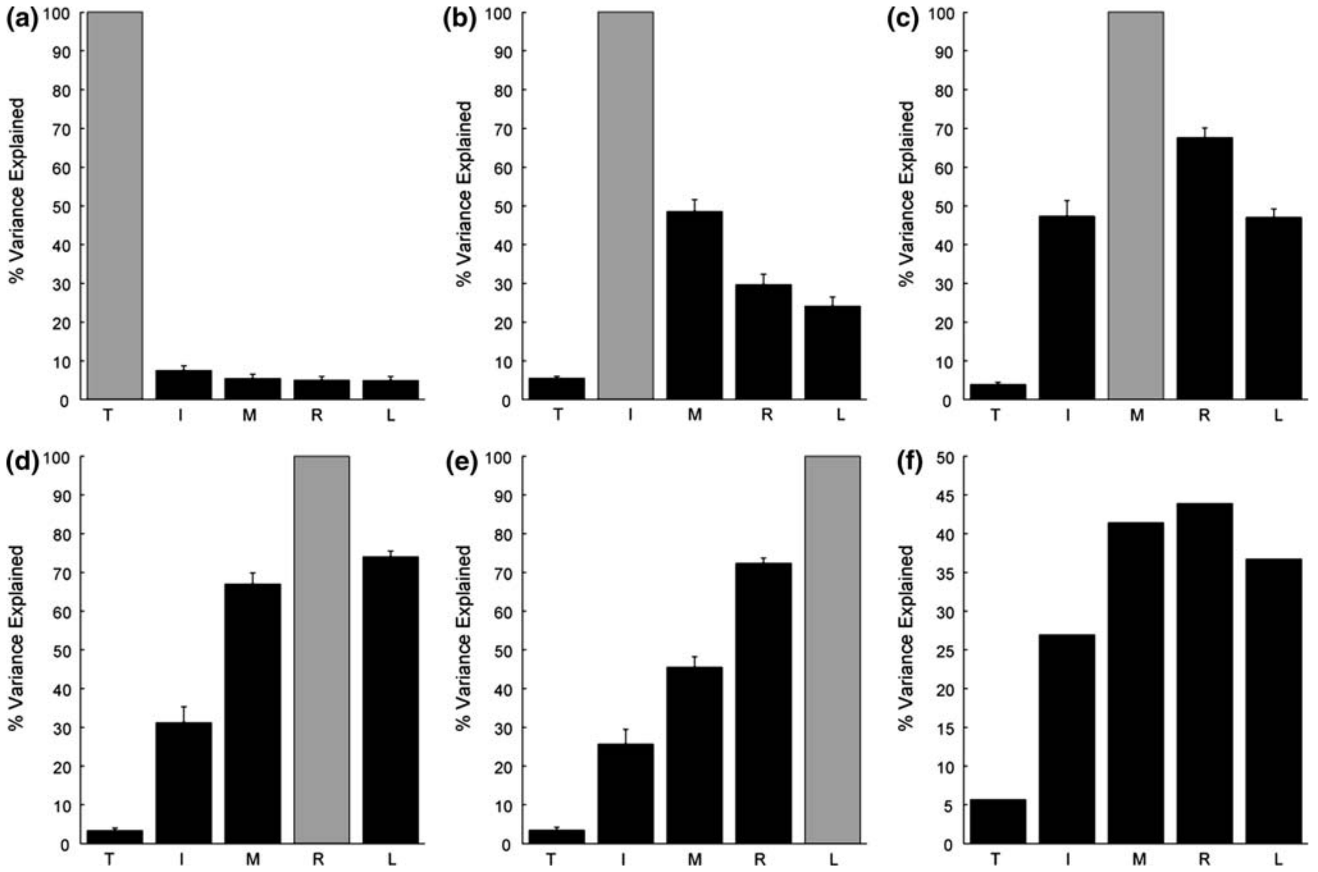

Fig. 5 Analysis of linear predictability of pairs of digits. Variance explained for each digit by a linear reconstruction of angular velocities based on one-on-one pairings with the other digits (subject mean and SE). *Grey bar* indicates 100% variance explained by pairing the digit with itself. **a** Thumb. **b** Index finger. **c** Middle finger. **d** Ring finger. **e** Little finger. **f** Mean variance explained for each digit (excluding the 100% self-pairing case)

the other four digits. The grey 100% bar in these figures shows the pairing of the digit with itself. The four black bars show pairings with the other digits. Results for the thumb (Fig. 5a) show that its movements are very difficult to predict by linear reconstruction from the movements of any of the fingers. Results for the fingers (Fig. 5b–e) show that the best linear reconstructions (highest coupling) are based on the movements of the immediately neighbouring fingers. In the case of the little finger (Fig. 5e) we see a progressive decrease in the percent variance explained as distance increases. The mean values for each of the digits are shown in Fig. 5f (the 100% self-pairing case is omitted). This analysis shows that while the thumb moves independently of the fingers, movements of the fingers are related to each other with decreasing strength as distance increases.

Analysis of digit movement times

The proportion of time during which each digit was moving provided another means of analysing the dataset (Fig. 6). Total movement time was similar for all digits (Fig. 6a) indicating that each digit was in motion for approximately the same amount of time. In contrast, the percentage of movements that were exclusive to each digit varied widely across the digits (Fig. 6b) and was highly correlated with our first linear predictability measure ($r = 0.96$; compare Fig. 4b with Fig. 6b). Specifically, percent exclusive movement was largest for the thumb, followed next by the index finger, then the little and middle fingers, and was smallest for the ring finger. As with our first linear predictability measure, percent exclusive movement was highly correlated with the Penfield Size ($r = 0.96$) and the Individuation Index ($r = 0.85$). Figure 6c shows the percentage of movements for each finger that are made exclusively with the thumb. This is expressed as the percentage of movements, which involve only the thumb and one finger. Almost half of such movements (48%) consist of movements of the thumb exclusively paired with the index finger. Figure 6d shows the results of a movement-time analysis for various combinations of the digits. As can be seen, one or more of the digits are moving 40% of the time. Of these movements, 88% include movements of one or more of the fingers, 66% include movements of the thumb, and 57% include combined movements of both the thumb and one or

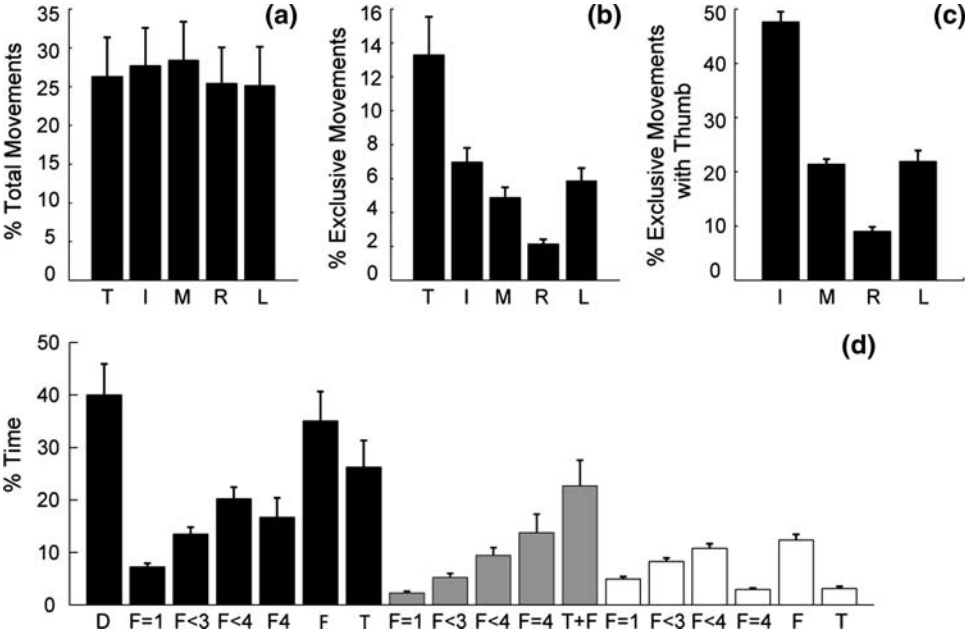

Fig. 6 Analysis of movement times of the digits. All graphs show subject mean and SE. **a** Total movements for each digit, calculated as the percentage time that the digit is moving. *T* thumb, *I* index, *M* middle, *R* ring, *L* little. **b** Exclusive movements for each digit, calculated as the percentage of the digit's total movements that occur while the other four digits are stationary. **c** Exclusive movements for each finger made while thumb is also moving, calculated as the percentage of total movements involving the thumb and any one finger. **d** Percent movement times for combinations of the digits, calculated as the percentage of total recording time. *D* any digit, *F* any finger, *F = 1* one finger, *F < 3* fewer than three fingers, *F < 4* fewer than four fingers, *F4* all four fingers, *T* thumb, *T + F* any finger and the thumb. *Black bars* represent total time for all digit movements. *Grey bars* represent finger movements made while thumb is also moving or thumb movements made while fingers are also moving. *White bars* represent finger movements made while thumb is stationary or thumb movements made while fingers are stationary

more of the fingers. The four fingers move together almost as frequently as do all combinations of fewer than four fingers (17% compared to 20%, respectively). Of those times when the four fingers are moving together, 82% of the movements also involve the thumb. In contrast, movements made by combinations of fewer than four fingers involve the thumb only 47% of the time. It is relatively rare for one finger to move in isolation (7%) and more than half of such movements (68%) involve the thumb. Although the thumb makes more isolated movements than any other digit (see Fig. 6b), most of its movements (86%) are nevertheless combined with movements of one of more of the fingers. These patterns of movements show that the hand most frequently moves as a unit and that isolated movements of individual digits are rare.

Discussion

We analysed a natural movement dataset collected from the right hand of human subjects who were free to behave spontaneously outside of the laboratory setting. The dataset represents almost 17 h of recording from six subjects and contains over five million hand postures. We applied a variety of statistical techniques to the dataset in order to characterize the hand movements made by humans during everyday life.

Dimensionality of the hand

From a PCA we found evidence for two major components in the movements of the hand. Both components were highly conserved across subjects and involved flexion/extension of the four fingers. Moreover, they were similar whether angular positions or angular velocities were analysed. This similarity almost certainly results from the fact that human movements are discrete with bell-shaped velocity profiles, which would tend to correlate variance in position with variance in velocity. Together, the two components explained over half of the variance in joint angular velocities and appeared qualitatively similar to those previously reported in laboratory-based studies of reach-to-grasp movements (Santello et al. 1998; Mason et al. 2001; Santello et al. 2002). In these previous studies, the characterization of PCs has been used to argue for synergistic control of the hand. This would suggest that reach-to-grasp movements or the synergies that mediate them may form an important component of the natural everyday tasks performed by the hand. Moreover, conservation across our six subjects suggests that these synergies may represent a fixed strategy for control of the hand. This is in contrast to suggestions by Todorov and Ghahramani (2004) who argue against the existence of fixed synergies in motor control. In their study, the first two PCs of the hand movement dataset varied between subjects and also between tasks. To account for this, they propose an optimal control strategy in which synergies are assembled dynamically in response to the specific requirements of each task. However, their conclusions are based on data from a limited number of tasks which may not have captured the full range and frequency of movements made by the hand on a day-to-day basis. We suggest that the frequency with which different movements occur will greatly influence the control strategies used by the motor system. This can only be determined from the study of natural, spontaneously generated movements.

Independence of the digits

Digit independence has previously been studied in a laboratory setting using tasks designed by the experimenter to measure the upper limits of independent movement. In a kinematic study of digit independence, Häger-Ross and Schieber (2000) asked subjects to move each digit in turn while keeping the other digits completely still. They developed a measure of independence for the digits (the Individuation Index), which quantified the ability of each digit to move without associated movements of the other digits. This measure could not be applied to our dataset because it requires knowledge of which digit the subject intends to move. Instead, we developed a measure of digit independence based on linear predictability. Our measure was highly correlated with Hager-Ross's Individuation Index and importantly preserved the ranked order for the digits, with the thumb being the most independent of the digits, the index finger the most independent of the fingers and the ring finger the least independent of all. While previous studies have employed artificial tasks specifically designed to measure the limits of independent movement, we confirm the pattern of digit independence in the natural everyday use of the hand.

Neural representation of the digits

The issue of digit independence is related to questions about the allocation of neural resources in cortical representations of the digits. Hypothetically, if two digits were always perfectly correlated in their movements (scoring 0% by our independence measure) then it would be more efficient to have a single neural representation to drive both of them. Similarly, if the movements of two digits were always completely independent of each other (scoring 100% by our measure) they would require two separate non-overlapping neural representations. In our analysis the digits scored between these extremes suggesting that the neural control may be mediated by both independent and overlapping populations of neurons. Moreover, it should be possible to predict the extent of these independent and overlapping populations based on the pattern of digit independence. In monkey, for example, overlapping representations of the digits are very common; the majority of the cortico-motoneuronal (CM) cells activate several different hand muscles (Lemon 1993). Digit independence is low in these primates. In humans the only comparable electrophysiology study is that of Penfield and Broldrey (1937), which used surface stimulation of the cortex to estimate the size of the cortical representations for different parts of the body. Although some of Penfield's conclusions have been questioned (for example Indovina and Jerome 2001; Schieber 2001), we nevertheless found a high correlation between our measure of digit independence and Penfield's estimates of the size of each digit's representation. If this result can be confirmed using contemporary methods, it would suggest that the allocation of neural resources for each digit in motor cortex may be correlated with the capacity for independent movement.

Coupling of the fingers

In previous studies, which rank the relationships between the fingers, it has been reported that immediately neighbouring fingers are most closely correlated. Zatsiorsky et al. (1998) asked subjects to produce force at a single instructed finger and report enslaving effects by which involuntary forces were produced at all non-instructed fingers. The effects were always largest for the immediate neighbours of the instructed finger with more distant fingers exhibiting smaller enslaving effects. Similarly, Aoki et al. (2003) found that all fingers produced involuntary movements during a single finger-tapping task. These involuntary movements were always greatest for the fingers immediately adjacent to the tapping finger. Santello et al. (2002) used the CyberGlove (15 sensor version) to study the dynamic evolution of hand posture during reach-to-grasp movements. They found positive correlations between MCP joint pairs and PIP joint pairs for the fingers and these were highest between adjacent fingers. This topography of finger interactions, with the movements of immediately neighbouring fingers being most correlated, emerged from our dataset in a number of analyses. In an analysis of homologous flexion/extension joints of the fingers (MCP, PIP, DIP), correlations were highest between immediately neighbouring pairs of fingers, falling off progressively with more distant pairings. In our paired linear predictability analysis, the topographic relationship between the fingers was also evident, with the immediate neighbours of each finger explaining most of the variance in that finger's movements, falling off progressively for more distant pairings. This is especially evident for the little finger, although the trend is present for each finger.

The thumb

The musculoskeletal anatomy of the thumb is unique, relative to the fingers (Imaeda et al. 1992) and relative to the thumbs of other primates (Tuttle 1969; Marzke 1992). Mechanically, the limitations on the independent movement of the thumb appear to be negligible compared to the fingers (Lang and Schieber 2004). Moreover, clinical studies of stroke patients suggest subtle differences in the neural architecture of the thumb compared to the fingers (Lang and Schieber 2003; but see also Raghavan et al. 2006). Not surprisingly, the thumb emerged as a special digit in a number of our analyses. In our first linear predictability measure, which characterized overall digit independence, the thumb ranked highest, scoring almost twofold higher than the index finger. In our second linear predictability measure, which characterized the coupling of movements between pairs of digits, the pattern for the thumb was very different to that of the fingers. In this analysis, the movements of the thumb were similarly independent of each of the four fingers, whereas the fingers exhibited a topographically scaled pattern of coupling. In our movement time analysis, although the thumb did not differ from the fingers with regard to the total time it was moving, its percentage exclusive movements were twofold more frequent than those of the index finger. In our PCA, the first two components (which explained over half the variance of the dataset) involved the four fingers to the exclusion of the thumb. Conversely, the thumb's contribution to higher order components was in many cases to the exclusion of the four fingers. This suggests the existence of synergies involving the fingers, which exclude the thumb and also the existence of synergies involving the thumb, which exclude the fingers.

The fingers

In contrast to the unique patterns of movement for the thumb, movements of the four fingers were shown to be closely related. Correlations between flexion/extension joints across the fingers were highest proximally at the MCP joints and decreased progressively at the more distal PIP and DIP joints. Conversely, correlations between the flexion/extension joints within each finger were low for the MCP joint and very high between the PIP and DIP joints. These patterns of joint correlations were the same for each finger. The high correlations between the PIP and DIP joints of the fingers justify assumptions made in previous studies (Santello et al. 1998). The fingers were shown to work together in the first two components of our PCA. This cooperative behaviour of the fingers was also highlighted in our movement time analysis. A significant proportion (42%) of the movements of the hand involved the four fingers moving together. Such movements were almost as frequent as any combination of three or fewer fingers. Moreover, when the four fingers moved together, they involved the thumb for a large proportion of the time (82%). This supports the proposal that the four fingers work together to form a "virtual finger" in opposition to the thumb (MacKenzie and Iberal 1994). It also suggests that whole-hand movements, involving all the digits, form an important part of the behavioural repertoire of the hand. Indeed, 35% of all movements in the dataset were whole-hand movements. With regard to the fingers, the index finger emerged as unique in a number of analyses. Its movements were the most independent among the fingers, scoring twofold higher than its nearest rival in our digit independence measure. In addition, of the 6% of movements, which involved the thumb and a single finger, almost half (47%) of such movements involved the index finger. This special relationship between the thumb and index finger is suggestive of the precision tip pinch grip by which especially small objects are manipulated (see review by Jones 1997; Jones and Lederman 2006).

Factors contributing to the pattern of digit independence

It is likely that both mechanical and neural factors contribute to the pattern of digit independence reported here (see review by Schieber and Santello 2004). For example, mechanical factors limiting independence of the fingers may include coupling by the skin, soft tissues and tendons. This was examined by von Schroeder and Botte (1993) using the hands of cadavers. They measured the angles of the MCP, PIP and DIP joints of the four fingers while applying traction to the extensor tendons of single fingers. Traction of single finger tendons resulted in extension of all fingers. The effect was always highest for the immediate neighbours of the actively extended finger, falling off progressively for more distantly removed fingers. This suggests that mechanical factors contribute to the pattern of digit coupling we found for the fingers. In a more recent study, Lang and Schieber (2004) measured joint angles of the digits during externally applied flexion and extension. They show negligible coupling between the thumb and the fingers, consistent with our findings. Moreover, the pattern of mechanical coupling they report for the fingers also matches our results, again highlighting a role for mechanical factors. Studies, which have used

EMG to examine the activity of the extrinsic finger muscles, have also reported this pattern of coupling between the fingers. For example, Kilbreath and Gandevia (1994) made intramuscular EMG recordings from the flexor digitorum profundus (FDP) muscle, one of the four-tendon extrinsic hand muscles, which flex the fingers. Subjects lifted small weights individually with each of the fingers. Regions of the muscle serving non-lifting fingers were also active and the level of this activity was scaled based on proximity to the lifting finger. In a more recent study, Reilly and Schieber (2003) also made intramuscular EMG recordings from FDP and similarly report activity in regions of the muscle serving non-task fingers. They suggest that incomplete division of the muscle into separate functional compartments limits the ability of the fingers to move independently.

Neural factors also contribute to the pattern of independence of the digits. Exclusive movement of a single digit is complicated by the fact that many of the muscles involved act on multiple joints and multiple digits (see Lemon 1997). The neural control of individuated digit movements therefore requires activation of the muscles directly involved in moving the digit as well as muscles required to prevent unwanted movements at the other digits. Movement of a single digit likely requires a pattern of activation and inhibition of the muscles acting on every digit and individual neural controllers for each digit would be required to communicate extensively (Schieber and Santello 2004). In the primary motor cortex of monkeys, single neurons are active during multiple digit movements and such neurons are dispersed through the entire representation of the hand (Poliakov and Schieber 1999). In humans, fMRI studies suggest partial segregation of digit-specific regions in primary motor cortex (Kleinschmidt et al. 1997; Beisteiner et al. 2001) and this may contribute to the ability of humans to individuate digit movements. Moreover, clinical studies of the effects of small cortical lesions also suggest some degree of digit specialization in primary motor cortex (Schieber 1999; Kim 2001).

Conclusion

We have measured the statistical properties of natural movements of the human hand. Our results generally support those obtained from laboratory-based studies. However, because such studies necessarily employ a limited set of tasks, it is important to verify their conclusions using natural movement datasets. Specifically, we have verified the pattern of digit independence in the everyday use of the hand and shown that many aspects of natural hand movements have been well characterized by previous studies of the reach-to-grasp movement.

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