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Matching object size by controlling finger span and hand shape

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Abstract

The ability of human subjects to accurately control finger span (distance between thumb and one finger) was studied. The experiments were performed without visual feedback of the hand and were designed to study the dependence of accuracy on object size, shape, distance, orientation and finger configuration. The effects of finger combination and sensory modality used to perceive object size (vision and haptics) were also studied. Subjects were quite proficient at this task; the small errors tended to be predominantly negative, *i.e.*, finger span < object size. The thumb-little finger combination was less accurate than the other finger combinations, irrespective of the sensory modality used. Subjects made larger under-estimating errors when matching the size of cylinders than when matching cubes and parallelepipeds. No effect of viewing distance, object orientation and finger configuration was found. Accuracy in matching object size was not dependent on the sensory modality used. The question of how the individual degrees of freedom of the fingers and thumb contributed to the control of finger span was also addressed. Principal components analysis showed that two components could characterize the hand postures used, irrespective of object size. The amplitude of the first principal component was constant, and the amplitude of the second scaled linearly with object size. This finding suggests that all of the degrees of freedom of the hand are controlled as a unit. This result is discussed in relation to the 'virtual finger' hypothesis for grasping.

Key words: *finger span, hand, grasp, degrees of freedom, principal components*

Introduction

Human subjects make large and consistent errors when they are asked to make proximal arm movements under conditions where visual feedback is not available, i.e. when the arm and the target are not viewed simultaneously. For example, subjects make large errors in distance when they are asked to put their finger at the remembered location of a target (Soechting and Flanders, 1989a,b) and they also make substantial errors when they are asked to utilize proprioceptive information to define the location of a point in space (Helms Tillery *et al.*, 1991). Similarly, subjects make predictable errors when they are instructed to orient a hand-held rod, using the wrist, to match the orientation of a rod presented at various locations in space (Soechting and Flanders, 1993; Flanders and Soechting, 1995). Such errors have been used to infer the frames of reference in which information may be represented (cf. Flanders and Soechting, 1995; Soechting and Flanders, 1992) and some of the putative stages in visuomotor processing (Flanders *et al.*, 1992).

In this paper we address the question: are there consistent errors when subjects are required to control the posture of the fingers? Specifically, we seek to determine how accurately subjects can control finger span, that is the distance between one finger pad and the opposing thumb, in response to information that is presented visually or proprioceptively. Published work (Chan *et al.*, 1990; Jeannerod and Decety, 1990; Chieffi and Gentillucci, 1993) indicates that subjects are quite accurate on the task of matching finger span between index finger and thumb to the size of objects presented visually, the slope of the relationship between the two variables being close to unity. Chan *et al.* (1990) also found that subjects were equally able to match the size of objects sensed haptically with the other hand.

Here we extend this previous work by addressing the question of whether the accuracy in scaling finger span depends on which finger is coupled to the thumb. The present experiments were also designed to include other factors that may affect accuracy in matching object size: the sensory modality used (vision or proprioception), and object characteristics (size, shape, spatial location and orientation). Since there is no unique relation between finger span and the posture of the finger and thumb, we also tested whether consistent errors were introduced when this factor was varied. In contrast to studies on the control of the proximal degrees of freedom of the arm, where subjects can and do make appreciable errors (cf. Soechting and Flanders 1989a,b), subjects were quite accurate in controlling finger span under all of the experimental conditions. A subsequent experiment, in which we

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determined how the posture of the entire hand was scaled to object size, provided a kinematic basis for what, to us, was a surprising finding. In particular, in this third experiment we found that subjects controlled all of the degrees of freedom of the hand as a unit, and that there was a simple linear relation between each of the joint angles and the object's size.

Materials and methods

Overview

In all of the experiments, subjects were required to match object size (the length of one face of a cube or the diameter of a cylinder) by adjusting either the finger span (the distance between the right thumb and one finger) or by shaping the entire right hand as if to grasp the object. We report results of three experimental protocols: matching finger span to a visually perceived object size ('vision', experiment 1); matching finger span to a haptically perceived object size ('haptics', experiment 2); matching object size by shaping the whole hand ('whole hand', experiment 3). Translucent solids were used for all the protocols. A screen blocked the view of the right hand. In the 'haptic' experiments the left hand, used to sense object size, was also not in view.

A total of eleven right-handed subjects (seven males and four females) took part in the experiments, their age ranging from 25 to 43. Five subjects participated in each experiment (except for experiments 1e and 2b, in which only four subjects were used). Three subjects took part in all the experiments. All subjects gave informed consent and the protocols were approved by the Institutional Review Board of the University of Minnesota.

Apparatus

Experiments 1 and 2. Two linear position transducers (model LT, Data Instruments Inc., Acton, MA) were used to measure finger span. The transducers were mounted to a frame such that the movement of the two shafts was collinear. The fingertips (medial and lateral surface) of the thumb and one of the other fingers were fixed to the transducer shafts by adjustable screws. Markers were placed on the fingertips to assess small changes in finger position relative to the thumb screws. When a detectable misalignment between the markers and thumb screws occurred during the experiments, the position of the finger tip was adjusted and the trial was repeated. The subject's elbow and wrist were supported, with the forearm horizontal and the upper arm vertical, the arm in the parasagittal plane passing through the shoulder and the hand in a semi-pronated position. Subjects were asked to assume a comfortable finger posture prior to the presentation of the objects. No other instructions were given with regard to the initial finger posture. Data collection commenced after the subjects indicated verbally that they had completed their movement.

The output of the two transducers was sampled at 12 ms intervals and 20 samples were averaged to calculate the distance between them. Each of the transducers was calibrated separately and a final calibration was performed at the end of each experiment by asking subjects to adjust the finger span so as to make contact with a small cube (3.1 cm size). For the protocol studying the effect of finger configuration, finger span was measured by a Vernier caliper.

Experiment 3. Hand posture was measured by 17 sensors embedded in a glove (CyberGlove, Virtual Technologies, Palo Alto, CA) worn on the right hand (Soechting and Flanders, 1997). The degrees of freedom (dfs) measured were the joint angles at the metacarpal-phalangeal (mcp) and proximal interphalangeal (pip) joints of the four fingers and the angle of abduction between adjacent fingers. For the thumb, the mcp and pip angles were measured, as was the angle of thumb rotation about an axis passing through the trapeziometacarpal joint of the thumb and index mcp joint. Wrist pitch and yaw angles were also recorded. The angle at each df was defined as 0° when the wrist was in neutral position, with all the digits extended and together. Positive values at the wrist pitch and yaw dfs denote wrist flexion and abduction, respectively. Positive values at the remaining dfs denote flexion and abduction between the digits. At the thumb, positive values of thumb rotation denote internal rotation. The spatial resolution of the CyberGlove was $< 0.1^{\circ}$.

Protocols

Experiment 1 ('vision')

(1a) Effect of object size and finger combination. Subjects viewed cubes located in the subjects's midsagittal plane at a distance of 40 cm, and then adjusted the distance between the thumb and one of the four fingers to match the size of the cube. Nine cubes were used, ranging from 0.5 to 12.4 cm to a side, in intervals of approximately 1.5 cm. Each of the cubes was presented four times in random order. (The protocols for subsequent experiments were the same, except as noted.)

(1b) Effect of object shape. Three different shapes were used: cubes, parallelepipeds and cylinders. The same three sizes were used for each: 1.9, 3.1 and 5.0 cm (length of one side or diameter). The cylinders had a height of 5 cm and the parallelepipeds an aspect ratio of 3:1. In this and the following protocols (1c, 1d and 1e) finger span for two finger combinations was examined: the thumb and the index or the little finger.

(1c) Effect of object distance. Cubes were presented at three distances (28, 45 and 62 cm) from the trunk. Five cube sizes (3.1–9.5 cm) were used.

(1d) Effect of object orientation. In the standard orientation (protocols 1a–c), the faces of the cubes were parallel to the frontal and horizontal planes, i.e. opposition axis of the hand was in alignment with the cube. In protocol 1d, cubes were rotated by 45° about the either the vertical or the antero-posterior axis. Eight cubes, ranging from 0.5 cm to 11.0 cm, were used.

(1e) Effect of finger configuration. Subjects were instructed to match finger span to cube size in one of two constrained finger postures. The postures were defined by the distance d between the opposition axis and the index mcp joint. One ($d \sim 7.5$ cm) corresponded to the posture used in other protocols ('control' posture); in the other posture ($d \sim 6.0$ cm, 'test' posture), there was a larger degree of flexion at the mcp and pip joints. The distance d was controlled by fixing the elbow and wrist relative to reference points on the support surface. Three cube sizes (1.9, 3.1 and 5.0 cm) were used, maximum finger span being more limited at smaller values of d.

Experiment 2 ('haptic')

(2a) Effect of object size and finger combination. After the experimenter placed cubes between the subject's thumb and index finger of the left hand, the subject was asked to grasp the cube and to match the finger span of the right hand to its perceived size. Subjects were not allowed to manipulate the cubes after making contact with them. The same nine cubes as in experiment 1a were used for each of the four fingers coupled to the thumb. Neither hand was in view.

(2b) Effect of finger configuration. The same protocol as in *1e* was used except that object size was sensed haptically by the thumb and index finger of the left hand. For the left hand the distance d between the opposition axis and index mcp joint was kept fixed at 7.5 cm by placing the edges of the cubes at the same locations for each trial and it was either 6.0 cm or 7.5 cm for the right hand.

Experiment 3 ('whole hand')

The protocol for this experiment was the same as that in experiment 1a, with the exception that subjects were instructed to shape the right hand (which was unconstrained) into the posture appropriate for holding the object. At the end of the experiment, we asked subjects to grasp each of the cubes. When grasping the cubes, subjects kept the same arm position used for the matching task, and the cubes were placed within the finger aperture.

Data analysis

Standard statistical measures (ANOVA and linear regression) were used to test for significant effects of each of the factors on the error. The 0.05 significance level was chosen. Tukey's post-hoc t-test was used when significant main effects were found. To determine the degree of similarity among the hand postures used to match different object sizes, we performed a principal component analysis (Glaser and Ruchkin, 1976) on the kinematic data for each subject. We first characterized the static hand posture as a 'waveform' of the values measured from the 17 dfs of the CyberGlove. We then computed principal component (PC's) from the waveforms associated with the nine cubes. The PCs were computed using the eigenvalues and eigenvectors of the matrix of correlation coefficients between each of the 9 waveforms (see Soechting and Flanders, 1997, eq. 1). Since only two PC's were required to characterize hand posture, this method

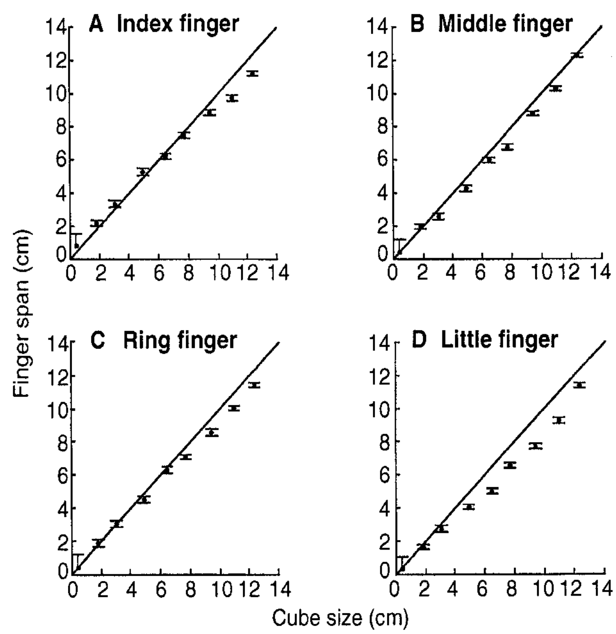


FIGURE 1. Matching cube size by different finger combinations. 'Vision' condition. The relationship between cube size and finger span is shown for the thumb-index (A), thumb-middle (B), thumb-ring (C) and thumb-little (D) finger combinations. The data are averages of 4 trials from each of 5 subjects. The error bars denote the standard deviations normalized with respect to cube size. The 45° line, indicating a one-to-one relationship between finger span and cube size, has been drawn for comparison. Subjects tended to make larger negative errors (finger span < cube size) when matching larger cube sizes. This tendency is particularly evident in the thumb-index finger and thumb-ring finger combinations (A and C, respectively). The normalized variable error tended to decrease with increasing cube size, indicating that the variability in the performance did not increase at the same rate as cube size (see text for further details).

TABLE 1. 'Vision' condition—relationship between finger span and cube size

Finger	r^2	Slope	Slope (intercept = 0)	Constant error Avg (± SD)	NVE Avg (± SD)	Slope NVE vs cube size
T-I	0.929	0.900	0.933	− 0.35 (1.05)	0.19 (0.21)	− 0.010*
T-M	0.884	0.934	0.924	− 0.52 (1.34)	0.24 (0.13)	− 0.020**
T-R	0.877	0.908	0.912	− 0.55 (1.37)	0.19 (0.06)	− 0.011**
T-L	0.906	0.874	0.844	− 1.07 (1.20)	0.13 (0.07)	− 0.001 (ns)

NVE, normalized variable error;** $p < 0.01$; *$p < 0.05$.
The r^2 and the slope of the relationship between finger span and cube size were calculated for the pooled data from 5 subjects and for each finger combination. The slopes of the regression lines were also computed after forcing the intercept to zero. The average constant and variable errors are also reported for each finger combination. The variable error was normalized by cube size before averaging. The last column shows the slope of the relationship between the normalized variable error and cube size.

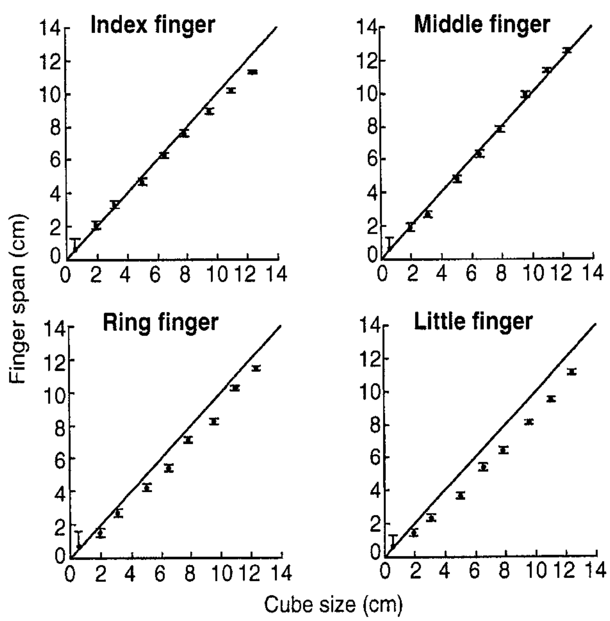


FIGURE 2. Matching cube size by different finger combinations. 'Haptic' conditions. The relationship between cube size and finger span is shown for the thumb-index, thumb-middle, thumb-ring and thumb-little finger combinations. Error bars denote standard deviations normalized by cube size. With the exception of the thumb-middle finger combination, subjects tended to make larger negative errors (finger span < cube size) when matching larger cube sizes. As for the 'vision' condition (Fig. 1), subjects were less accurate when using the thumb-little finger than any of the other three finger combinations; and the normalized variable error tended to decrease with increasing cube size (see text for further details).

affords a compact way to summarize a large body of data. The postures that correspond to each of the PCs were visualized using software (Persistence Of Vision Ray Tracer) to render a 3-D image of the hand.

Results

In all experimental conditions, we found that subjects were able to match cube size by accurately scaling finger span to object size. When matching cube size by shaping the whole hand, subjects scaled the amplitude of movement of all degrees of freedom in a linear fashion to object size. Principal components analysis showed that subjects adopted a default hand posture (1st principal component) for all cube sizes. To this posture, they superimposed a second hand posture (2nd principal component) whose amplitude scaled linearly with cube size.

In both 'vision' and 'haptic' conditions (Figs. 1 and 2, respectively), the finger span increased in an approximately linear fashion as a function of cube size when the index (I), middle (M), ring (R) and little (L) fingers were opposed to the thumb (T) (A, B, C and D in Figs. 1 and 2). The data in Figures 1 and 2 summarize the results from all 5 subjects, the error bars denoting average value of the subject's normalized variable error (NVE), i.e., the standard deviation normalized by cube size. Both the constant and variable errors were small. In the 'vision' condition, the constant errors for the cubes ranged from + 0.04 to − 1.89 cm with variable errors of comparable magnitude (ranging from ± 0.10 to ± 1.61 cm). Results obtained when subjects sensed the size of the cubes by grasping them between thumb and index finger of the left hand ('haptic' condition, Fig. 2) were very similar to those obtained with 'vision'; constant errors ranged from 0.41 to − 1.50 cm and variable errors from ± 0.34 to ± 1.39 cm.

Matching cube size using visual information

In the 'vision' condition, constant errors tended to be negative, irrespective of the finger that was opposed to the thumb (Table 1) and the slope of the relationship between finger span and object size was slightly less than 1.0 (Table 1). The results for the little finger (Fig. 1D) differed from the results for the three other fingers. The magnitude of the constant error was significantly larger ($p < 0.01$) for T-L (Fig. 1D) than any of the other finger combinations and the slope of the regression line for T-L combination was significantly smaller ($p < 0.05$) than the slopes for the other three finger combinations. None of the other three slopes differed significantly from each other.

TABLE 2. 'Haptic' condition—relationship between finger span and cube size

Finger	r^2	Slope	Slope (intercept = 0)	Constant error Avg (± SD)	NVE Avg (± SD)	Slope NVE vs cube size
T-I	0.950	0.902	0.939	− 0.31 (0.89)	0.20 (0.18)	− 0.018**
T-M	0.952	1.033	1.012	0.08 (1.14)	0.21 (0.18)	− 0.015**
T-R	0.935	0.932	0.903	− 0.69 (0.99)	0.25 (0.25)	− 0.018**
T-L	0.922	0.894	0.849	− 1.06 (1.09)	0.21 (0.17)	− 0.010**

NVE, normalized variable error; $^{**}p < 0.01$; $^{*}p < 0.05$.
See Table 1.

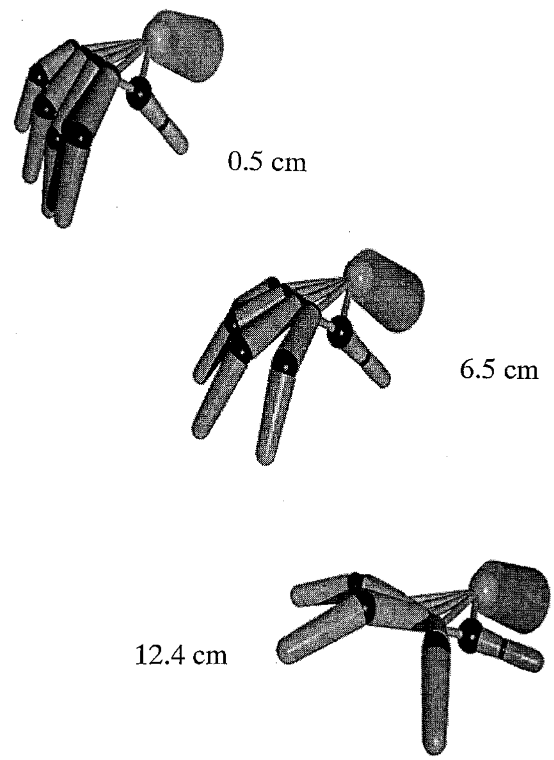


FIGURE 3. Hand postures used for virtual grasps. The 3-D images of three hand postures from on subject (S3) are shown for cubes of 0.5, 5 and 12.4 cm. The major effects of increasing cube size can be noticed at the metacarpal-phalangeal joints and at the abduction angles between the digits. Since motion at the distal interphalangeal joints was not transduced, the illustration depicts the fingers as if there were full extension at this joint.

The NVEs were similar for each of the fingers and tended to decrease with cube size, indicating that the variable error did not increase at the same rate as cube size. We found this tendency in all the finger combinations with the exception of T-L (see Table 1). (The NVE for the smallest cube size was excluded from the regression analysis because it was consistently much larger than the values obtained for the other cubes.)

To summarize, subjects tended to produce a finger span that was slightly smaller than the size of the cube. The errors for index, middle and ring fingers were very similar; that for the little finger was larger. Because this first experiment gave results that were very similar for the index, middle and ring fingers, only two combinations (T-I and T-L) were used in the following experiments which were designed to test a variety of putative factors that might decrease the accuracy with which finger span is controlled.

Only the shape of the object (experiment 1b) had an effect on the relationship between finger span and object size; viewing distance (1c), the object's orientation (1d) and the configuration of the fingers (1e) did not. When subjects were asked to match the size of three differently shaped solids (cubes, parallelepipeds and cylinders), they tended to underestimate the size of cylinders (diameter) by a slightly larger amount than the size of cubes and parallelepipeds (length of one face). This was found for both the index as well as little finger, the average error of the two fingers being 96% and 40% larger than the errors in matching cubes and parallelepipeds, respectively. The errors in matching cylinders were significantly larger ($p < 0.05$) than those for cubes and parallelepipeds.

Subjects made very similar errors in matching cube size regardless of object distance and orientation. There was no significant effect of viewing distance on the errors made when the object was located at 28, 45 and 62 cm from the subject ($F(2,570) = 0.11$, $p = 0.9$). Likewise, rotating the cubes by 45° about the vertical or antero-posterior axis had no significant effect on the errors in matching finger span to cube size ($p = 0.45$ and $p = 0.83$, rotation about horizontal and vertical axes, respectively). Note that when the cubes are rotated, the opposition axis used to measure finger span was constrained to remain horizontal in the frontal plane and no longer matched the orientation of the opposition axis with which the object would be grasped.

Since there is no unique relationship between finger joint angles and finger span, we also tested whether or not altering this relationship would affect subjects' accuracy on the matching task. It did not. When we changed the distance d between opposition axis and index finger mcp joint from 7.5 cm to a more flexed posture with $d = 6$ cm, there was no significant effect on the error of matching finger span to object size.

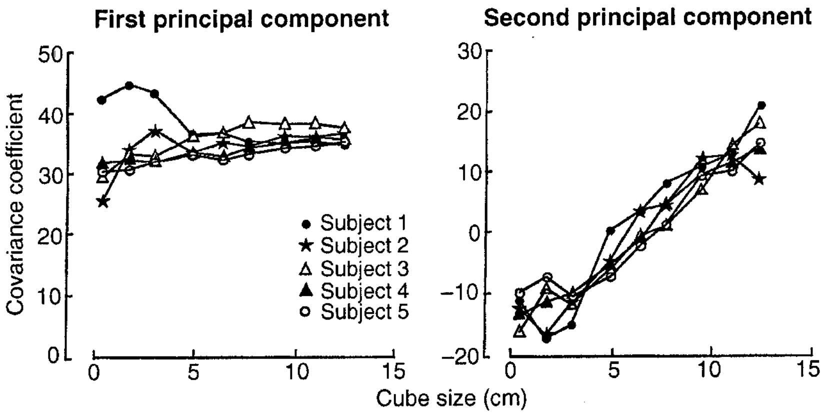


FIGURE 4. Covariation between the first principal component and hand postures. The covariance coefficients between the first two principal components (A and B, respectively) and the hand posture used for each cube size (virtual grasps) are plotted against cube size. The amplitude of the first principal component (A) remains fairly constant across cube sizes, whilst the second principal component (B) scales linearly with cube size.

Matching cube size using haptic information

When subjects sensed object size by grasping the cubes between the index finger and thumb of the left hand, the results were very similar to those obtained when subjects viewed the objects (Fig. 2 and Table 2). With the exception of the thumb-middle finger (T-M) combination where subjects were more accurate in the 'haptic' condition, the two sensing conditions yielded no significant differences in the size of the constant error or in the slope of the relation between finger span and cube size (Table 2). As was the case for the 'vision' condition, the slope of the relation between finger span and cube size was smallest for T-L and differed significantly ($p < 0.05$) from the slopes for the other fingers.

We repeated the experiment (1e) in which the finger configuration was manipulated, now requiring subjects to sense cube size haptically with their left index finger ($d = 7.5$ cm) and to match it with the finger span of the right T-I combination under two conditions: same posture (i.e., $d = 7.5$ cm) or with the fingers more flexed ($d = 6$ cm). There was no significant difference in the errors made under the two conditions. The modality used to sense object size (vision or haptic) also made no difference.

TABLE 3. Regression analysis—relationship between angular displacement and cube size.

	Degrees of freedom	r^2
	TR	0.916
Thumb	TM	0.582
dfs	TP	0.310
	TA	0.694
	I	0.930
Metacarpal	M	0.860
dfs	R	0.620
	L	0.496
	I	0.378
Interphalangeal	M	0.637
dfs	R	0.637
	L	0.792
	I-M	0.802
Abduction angles	M-R	0.664
	R-L	0.718

The table shows the r^2 of the relationship between angular displacement at each degree of freedom and cube size. The thumb dfs are the angles of thumb rotation (TR), at the metacarpal-phalangeal joint (TM), at the proximal interphalangeal joint (TP) and the abduction angle of the thumb (TA). I, M, R and L denote the index, middle, ring and little fingers, respectively. The r^2 shown were calculated from the averaged trials ($n = 4$) for each subject and averaged across subjects.

Matching cube size by shaping the whole hand

In the first two experiments, one finger and the thumb were constrained to move along a particular axis and motion of the other fingers was not transduced. The third experiment was aimed at determining how displacement at the various degrees of freedom of the hand was coordinated to control finger span. We found that a very simple linear relation held between the finger joint angles and the object's size. Furthermore, the results suggested that in this task, all of the degrees of freedom of the hand are controlled as a unit.

Figure 3 shows the postures of the hand assumed by one subject (S3) while grasping virtual cubes of three different sizes. (Since motion at the distal interphalangeal joints were not transduced, the illustration depicts the fingers as if there were full extension at these joints.) As cube size increased, there was more extension at the mcp joints of all the digits, as well as an increase in the abduction angles between the digits for this subject. Flexion at the pip joints depended little on cube size. In general each of the degrees of freedom (dfs) scaled linearly with cube size. This was demonstrated in two ways. First, a linear regression analysis on the data (i.e., angle at each df vs cube size) yielded r^2 values that averaged

TABLE 4. Principal components of virtual and real hand postures

Subjects	Virtual grasp			Real grasp
	First principal component	Second principal component	First principal component	Second principal component
S1	90.6	8.7	87.8	10.4
S2	89.4	8.4	78.0	13.5
S3	90.6	8.5	92.5	6.5
S4	91.7	7.4	88.2	8.9
S5	93.0	6.3	90.8	6.6

The variance explained by the first and second principal components are shown for the virtual and real grasps performed by each subject. In both tasks, two components were sufficient to describe the hand postures used for each cube size.

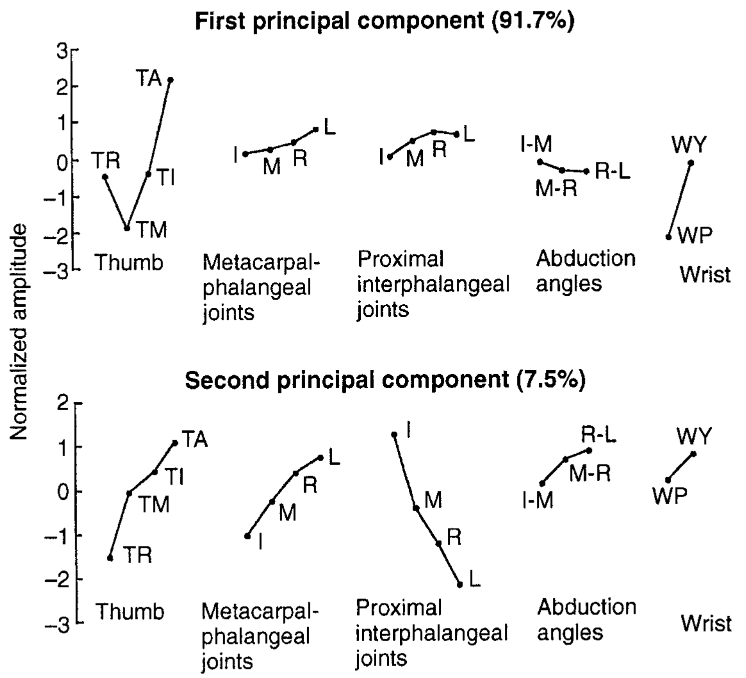
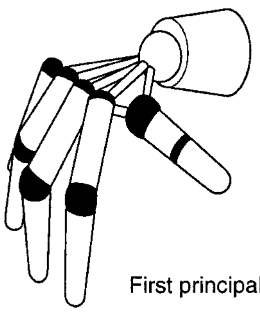


FIGURE 5. First and second principal components of virtual hand postures. The upper and lower panels show the first and second principal components, respectively, of nine hand postures used for virtual grasps by one subject (S3). Each principal component represents a postural pattern of the 17 degrees of freedom. These have been ordered (see labels), I, M, R and L denoting the index, middle, ring and little fingers, respectively. The dfs of the thumb are the angles of thumb rotation (TR), at the metacarpal-phalangeal joint (TM), at the interphalangeal joint (TP) and the abduction angle of the thumb (TA). The amplitude of each principal component is normalized, positive deflection indicating flexion.

0.669 over all degrees of freedom and subjects, with a range of 0.310–0.930 (Table 3). Second, we performed a principal component (PC) analysis on the data for each subject. The first two PCs sufficed to characterize the variations in hand posture found in this experiment, since they accounted for 98–99% of the variance (Table 4). The first PC defined a default posture, since its amplitude remained relatively constant across cube sizes for all subjects (Fig. 4A) and the amplitude of the second PC tended to scale linearly with cube size (Fig. 4B).

The upper and lower panels in Figure 5 show the 'waveform' of the first and second PC, respectively, from subject S4. The scale of the y-axis is expressed in normalized form. The data shown were normalized by first assigning the value of zero to the mean amplitude of all the dfs, and expressing the amplitude of each df as standard deviations of the mean amplitude. Positive and negative values indicate flexion and extension, respectively. The first PC (upper panel) is characterized by similar values of extension at the mcp and pip joints of each of the four digits, as well as a relatively constant amount of abduction between pairs of digits. This default posture was similar for all subjects, the inter-subject correlation coefficients ranging from 0.707 to 0.940 (mean 0.834, SD ± 0.072).

As can be deduced from the second PC (lower panel, Fig. 5), angular displacement at each of the mcp and pip joints scales differently with cube size. In particular, there is an orderly progression from the index to the little fingers. In this subject, the



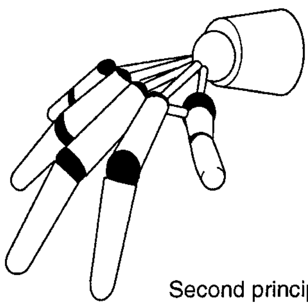


FIGURE 6. Hand postures corresponding to the first and second principal components. The first and second principal components shown in Figure 5 are illustrated in a perspective view. The amplitude of the first principal component is the one used by this subject when matching a cube of 6.5 cm, and the amplitude of the second principal component corresponds to the combination when an 0.5 cm cube was presented.

largest degree of extension at the mcp joint occurs at the index. At the pip joints, this order is reversed, the index finger being characterized by a larger degree of flexion than the rest of the fingers. For the thumb, the values for both the first and second PCs show large excursions about the mean. Different subjects used slightly different strategies in scaling grip aperture to cube size: the intersubject correlations of the second PC were more variable than for the first and were sometimes negative, ranging from -0.896 to 0.847 (mean -0.116, SD ± 0.745). Only half of the coefficients were larger than 0.8.

Figure 6 illustrates the hand postures corresponding to the first and second PCs shown in Figure 5. The values for the hand posture derived from a virtual grasp of the 6.5 and 0.5 cm cubes were used to scale the hand postures corresponding to the first and second PCs, respectively. At the mcp joint, there is a trend towards greater flexion as one progresses from the index finger to the ring finger for both PCs (see also Fig. 5). The opposite trend, namely a progression from flexion at the index finger to full extension at the little finger is evident at the pip joint for the second PC. Depending on the sign of the covariance coefficient (Fig. 4), the values represented by this second PC are either added to or subtracted from the first PC to reconstruct the hand posture for grasping cubes of various sizes.

At the end of each experiment, we asked subjects to grasp each cube to determine the extent to which the postures adopted for the virtual grasp correspond to the postures adopted in grasping the actual object. Even when subjects actually grasped the cubes, two PCs were adequate to explain most of the variance across the nine hand postures used (Table 4). We also found a similar trend in the amplitude of the two PCs as those observed for virtual grasps.

Discussion

Matching object size by finger span

None of the factors that we investigated (finger combination, object location, shape and orientation, and the modality used to sense object properties) had a major effect on the accuracy with which subjects matched cube size by adjusting finger span. Previous investigators had found that subjects were highly accurate in adjusting the finger span with the thumb—index finger combination, in response to a visual presentation of the object (Jeannerod and Decety, 1990; Chan *et al.*, 1990; Chieffi and Gentilucci, 1993) as well as when the object's size was sensed haptically (Chan *et al.*, 1990). Our results show that subjects are equally accurate when they use the index, middle or ring fingers in combination with the thumb, with a small decrement in performance when the little finger was used in combination with the thumb.

The task we have examined is not strictly comparable to motor tasks involving reaching and grasping objects, since the latter also involve a transport component and motion at the proximal joints of the arm, whereas in our experimental condition motion was restricted to the digits of the hand. Nevertheless, it may be instructive to interpret our findings from the perspective of the demands imposed during a grasping movement and to relate our findings to those on the evolution of the finger span during grasping movements. From this perspective, it is perhaps not surprising that the subjects' accuracy in matching finger span with the little finger was less than when each of the other fingers was used—the little finger is rarely used in a precision grip (Napier, 1956).

Subjects were as accurate in using haptic information as they were in using visual information. When the index finger of the right hand was used to denote finger span, the task could have been achieved by matching the respective joint angles of the two hands. However, the fact that similar results were obtained when the other fingers of the right hand were used, and when the experiments were done with the finger in a more flexed position (experiment 2b) would argue that subjects were actually able to 'compute' the finger span of the left hand, on the basis of proprioceptive and cutaneous information, and to use this information effectively to control the span of the right hand. The results of experiments 1e and 2b, in which subjects used a more flexed posture of their fingers, indicate that they were also able to cope effectively with the kinematic redundancy of the fingers to determine finger span. Clearly, such an ability would be most useful in tactile handling, for example in transferring objects from one hand to the other. It should be noted that our present results on the distalmost part of the arm differ from those on the proximal arm: subjects are quite accurate in matching the posture of the two arms as well as individual joint angles (Soechting and Ross, 1984; Flanders *et al.*, 1992), but they are highly inaccurate in using this information to determine the location of a point in space with respect to the body (Helms Tillery *et al.*, 1991, 1994).

There was no decrement in the performance when the opposition axis was not parallel to the faces of the cube (experiment 1d). One might have expected a tendency on the part of the subjects to overestimate the size of the cubes, i.e. to produce a finger span that would more closely correspond to the posture adequate to grasp the object if it were presented in that orientation. This expectation was based on our previous studies on orientating the hand to match the orientation of cylinders presented at arbitrary locations in space (Soechting and Flanders, 1993; Flanders and Soechting, 1995): subjects tended to orient the hand relative to the forearm and consequently made consistent and predictable errors when they were asked to dissociate the orientation of the hand in space from its location. In those experiments subjects used a precision grip to align a grasped cylinder and consequently the motion involved the fingers as well as the wrist. The present results indicate that finger span is controlled independently of the orientation of the hand. Such a result might be expected by the demands of grasping an object: during the initial course of the movement, the hand may not be aligned with the object to be grasped.

Matching cube size by shaping the entire hand

The results of the third experiment suggest that accurate control of finger span can be achieved in a fairly simple manner—linearly scaling the excursion at all of the joint angles with respect to the size of the object. The fact that we found a similar linkage among the movement amplitude of the digits for each hand configuration suggests that the global hand shape, rather than the movement at each joint, might be the controlled variable. A linkage among the degrees of freedom of the hand has also been reported for dynamic tasks, such as single digit flexion-extension (Schieber, 1991) and typing (Soechting and Flanders, 1997). These synergies originate from biomechanical as well as neural factors (Schieber *et al.*, 1997). A different model accounting for the control of the large number of dfs of the hand is the 'virtual finger' hypothesis (Arbib *et al.*, 1985). According to this hypothesis, the control of hand configuration is simplified by having a set of fingers, i.e., virtual fingers, working together as a functional unit.

The present results are not completely in accord with this hypothesis (see below). One principal component had the same amplitude, independent of cube size, defining a default posture. A second principal component, whose amplitude was linearly related to the size of the cubes, defined the means whereby finger span is regulated. As already noted, this finding implies that all of the dfs of the thumb and fingers are controlled in tandem. In view of this result, it should not be surprising that largely similar errors in adjusting finger span with various finger-thumb combinations were found in the first two experiments.

The fact that only two principal components were needed to define the posture of the hand also has a bearing on the 'virtual finger' hypothesis. The objects that we used in our experiments varied widely in size. One would expect that the smallest would be grasped using only the index finger in opposition to the thumb, the largest using all four fingers opposed to the thumb, and intermediate ones using intermediate combinations of fingers.

According to the hypothesis advanced by Arbib and his colleagues (Arbib *et al.*, 1985; Iberall *et al.*, 1986), one would therefore expect a different set of fingers to comprise a 'virtual finger' for different ranges of cube sizes. One might also expect a different postural synergy for each 'virtual finger' combination. Accordingly, one would expect that a larger number of principal components (one per 'virtual finger') would be required to describe the posture of the hand. Our results were contrary to this expectation. They imply that all of the dfs of the hand are controlled as a unit, at least for the present tasks, those of the fingers that are actually involved in the grasp as well as those which do not contribute directly to this task. Thus, while our results are in the spirit of Arbib's hypothesis, they also imply a refinement in its details.

Control of hand posture in grasping movements

There are similarities and differences between our results and observations made in the course of reaching and grasping movements. Maximum aperture between two fingers scales linearly to object size during the transport phase of grasping (Jeannerod, 1981, 1984; Marteniuk *et al.*, 1990; Jakobson and Goodale, 1991; Paulignan *et al.*, 1991b; Chieffi and Gentilucci, 1993; Castiello *et al.*, 1993), but with a slope that is appreciably less than unity (i.e., 0.77; Marteniuk *et al.*, 1990; Bootsma *et al.*, 1994). (Since the maximum aperture consistently exceeds the size of the object (the intercept is larger than 0), this finding does not necessarily imply an error in adjusting finger span during a reaching movement. These results can also be interpreted to mean that subjects employ a smaller safety margin for larger objects.) There are also similarities between our results and results during reaching movements: object location (Gentilucci *et al.*, 1991, 1992; Paulignan *et al.*, 1991a; Chieffi *et al.*, 1992) has no influence on finger span in either condition.

In summary our results indicate that subjects can adjust finger span to object size with a high degree of accuracy, independently of the orientation and location of the object relative to the hand. They also suggest that this process of scaling may be fairly simple, despite the large numbers of degrees of freedom involved in the task. At least for the restricted set of objects we investigated, all of the degrees of freedom of the hand appear to be controlled as a unit and each of the joint angles scaled linearly to the size of the object.

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