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RESEARCH ARTICLE

Control of Movement

Kinematic hand synergies differ between reach-and-grasp and functional object manipulation

A. Michael West Jr.[1] and Neville Hogan[2,3]

[1]*Department of Mechanical Engineering, Johns Hopkins University, Baltimore, Maryland, United States;* [2]*Department of Mechanical Engineering, Massachusetts Institute of Technology, Cambridge, Massachusetts, United States; and* [3]*Department of Brain and Cognitive Sciences, Massachusetts Institute of Technology, Cambridge, Massachusetts, United States*

Abstract

Humans possess a unique ability to manipulate tools to help us navigate the world around us. This ability is facilitated by the dexterity of our hands. However, millions lose this capability annually due to conditions like limb amputation or cerebral vascular accident (i.e., stroke). This great loss of human hand function has led to increased study of human hand action. Although previous research focused on coordinated hand motion, known as synergies, during reaching and grasping, manipulation of complex objects remains understudied. Specifically, we aimed to test two hypotheses: *1*) the number of synergies underlying manipulation is the same as those underlying reach-and-grasp, and *2*) the identity of synergies underlying manipulation is different from those underlying reach-and-grasp. To do so, we measured human hand motion during two experiments: *1*) during reach and grasp of a tool or object commonly used in wire harness installation and *2*) during manipulation of those objects and tools to install a wire harness on a mock electrical cabinet. Results showed that manipulation generally required more synergies than grasp. Comparison between reach-and-grasp and manipulation revealed a decrease in synergy similarity with synergy-order. Considering that higher-order synergies become significant during manipulation, it is important that we investigate these differences; this study serves as a point of entry to doing so. If we want our prosthetic and rehabilitative devices to restore hand function to those who have lost it, we must study hand function, specifically manipulation, and not just grasping.

NEW & NOTEWORTHY This study uncovers new insights into kinematic synergies during functional human hand manipulation of objects and tools, through the study of wire harness installation. It emphasizes the nuanced distinctions between functional hand manipulation and simple grasping, revealing that manipulation tasks require a greater number and distinct subset of hand synergies compared with simple grasp actions. This research marks a significant step toward appreciating the intricacies of hand coordination in complex tasks beyond grasping.

manipulation; motor control; physical interaction; synergy; tool use

INTRODUCTION

A hallmark of human behavior is the ability to use tools to help us manage our environment. For instance, in reading this paper, you have likely driven to the office, used a computer, and written notes—activities that all involve tools such as the car's steering wheel, the computer keyboard, and a pen. The remarkable dexterity of the human hand allows us to manipulate a wide variety of tools—a capability few other species possess (1–4).

Unfortunately, many individuals face injuries or conditions that impair or eliminate hand dexterity. For instance, ~15 million people globally and 800,000 Americans experience motor function loss due to cerebral vascular accidents (CVAs) each year, with hand function often being the most severely affected and recovering the least (5). In addition, 23 million people worldwide and ~700,000 Americans are living with hand amputations, a number projected to double in the United States by 2050 (6, 7). In a world designed for individuals with dexterous hands, the loss of hand function poses significant challenges, severely impacting the ability to perform everyday tasks.

Efforts to rehabilitate motor function after CVA and to design prosthetic hands have driven research into understanding

Correspondence: A. M. West Jr. (awest36@jh.edu).
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human hand motion. However, analyzing hand kinematics is challenging due to its more than 20 degrees of freedom across various joints (8). Insights from biomechanics and sensory-motor control can simplify this complexity by suggesting that many of these degrees of freedom are controlled in functional groups, influenced by biomechanical (and possibly neural) constraints. These functional groupings, commonly referred to as synergies, reduce the effective degrees of freedom in the hand. Mathematically, if $\theta \in \mathbb{R}^n$ denotes the configuration (joint angles) of the hand, a kinematic synergy may be described by a mapping $\theta = \varphi(\delta)$, where $\delta \in \mathbb{R}^m$ is a descending neural command with fewer dimensions than θ, i.e., $m < n$, and $\varphi(\cdot)$ is a time-invariant mapping such that $\theta(t) = \varphi(\delta(t))$. Under this assumption, a linear approximation of the kinematic mapping $\varphi(\cdot)$ can be obtained using dimensionality reduction methods such as principal component analysis (9) or singular value decomposition.

Inspired by Bernstein's work (10, 11), Santello et al. first studied kinematic synergies of the human hand in 1998. They found that two synergies accounted for more than 80% of the variance in hand posture during grasping of a set of 57 imagined objects (12). Similar findings have been reported in tasks involving object contact (13), reach-and-grasp (14), object manipulation (15), the American sign language (16), and even piano playing (17). For a comprehensive review, see Ref. 18.

Research suggests that this decrease in the hands' operational degrees of freedom may enable simpler control (19–27). Experimentally, it affords researchers a means to simplify kinematic analysis. However, much of the existing research focuses on simple grasping rather than object manipulation or functional tool-use. To effectively restore motor function in individuals with CVA or amputation, it is essential to study hand manipulation in the context of tool use. This raises an important question: do hand synergies differ between grasping and manipulation? This paper aims to explicitly compare grasp synergies and manipulation synergies.

Understanding human manipulation can also inform advances in robotic manipulation (28). Although robots are often used for simple pick-and-place tasks (29–32), more recent developments include limited forms of object manipulation, such as finger gaiting (33–38) and object repositioning within a grasp (39–41). However, few robots approach the dexterity and versatility of humans (42–45; for further discussion, see Refs. 28 and 46). Studying how humans manipulate tools during functional tasks could provide valuable insights to improve robotic systems.

Robotic control becomes even more challenging when manipulating deformable objects (47–52). A striking example is wire-harnessing, a manufacturing process involving the assembly of electrical cables into machinery such as aircraft and automobiles. Although robots excel at assembling rigid parts on an assembly line, the nonrigid nature of wire harnesses makes automation difficult (49). Consequently, wire-harnessing remains a manual task, creating a bottleneck in the assembly process. Interestingly, despite slower actuation, communication, and computation speeds, humans outperform robots in this task (53, 54). This paradox highlights the need to better understand how humans manipulate tools and deformable objects. To address this, we studied wire-harnessing to gain insights into the principles underlying human dexterity.

Motivated by the utility of dimensionality reduction techniques in studying hand kinematics, we formulated two hypotheses that compare both the number of reduced degrees of freedom and the specific forms of these synergies:

1) The number of synergies underlying manipulation is the same as those underlying reach-and-grasp.
2) The identity of synergies underlying manipulation is different from those underlying reach-and-grasp.

The first hypothesis arises from prior findings, particularly that two synergies can account for more than 80% of the variance in hand posture during grasping (12). The second hypothesis builds on the extensive literature on grasp synergies, highlighting the need to investigate hand manipulation during functional tool use—an essential focus if we are to restore motor function for individuals affected by CVA or amputation, rather than solely focusing on grasping.

To test these hypotheses, we measured human hand motion during two experiments, in the context of wire harness installation. In the first experiment, subjects reached for and grasped a tool or object commonly used in wire harness installation. In the second experiment, they manipulated those tools to install a wire harness on a mock electrical cabinet. Our results showed that more synergies were required to competently describe manipulation compared with reach-and-grasp. Moreover, upon comparing the kinematic hand synergies across reach-and-grasp and manipulation, we found that the difference was predominantly in the higher-order synergies. These findings underscore the importance of studying manipulation-specific synergies to inform therapeutic technologies that restore hand function—providing a crucial starting point for further research.

METHODS

Experimental Task

Seven adults (3 women and 4 men, aged 18–28 yr) with no history of neurological or musculoskeletal problems participated in this study. All participants were right-hand dominant. Before the study, participants were informed of the procedures and provided written consent. The study was approved by MIT's Institutional Review Board (MIT IRB Protocol No. 1909000007).

Data Acquisition

Each subject performed two tasks. The first, referred to as the Reach-and-Grasp Experiment involved reaching for, grasping, and picking up tools. Subjects were instructed to grasp each tool as if they were preparing to use it. The tools included a pair of scissors, a zip tie, a screwdriver, a wire harness with tied branched ends, and a wire harness with untied branched ends. Each tool was grasped four times. The second task, referred to as the Manipulation Experiment, emulated wire harnessing in a manufacturing setting. Subjects used the tools from the first task to install a wire harness onto a mock electrical cabinet (Fig. 1). This task consisted of five distinct steps. For each step, subjects were provided with verbal instructions, written guidelines, and a booklet containing a picture of the completed step. The steps were as follows:

Figure 1. The mock electrical cabinet after the Manipulation Experiment. The bottom half of the wire harness shows the zip ties used to secure its branched ends (*steps 1* and *2*). The top half features u-brackets for screwing the wire harness onto the cabinet (*step 3*). Red hooks were used to route the wire harness (*step 4*), and a three-dimensional (3-D)-printed socket above the rightmost hook allowed subjects to plug in the wire harness connector (*step 5*).

1) Zip tie the branched ends of the wire harness at three specified points.
2) Use the scissors to cut off the excess tips of the Zip ties.
3) Use the U-brackets, provided screws, and screwdriver to screw the wire harness into the top of the mock electrical cabinet.
4) Route the wire harness through the hooks on the mock electrical cabinet.
5) Plug the connector into the socket on the mock electrical cabinet.

These steps were chosen to simulate an assembly task that requires both dexterous manipulation of a deformable object and functional tool use.

Hand posture was measured during the tasks using a CyberGlove (Virtual Technologies, Palo Alto, CA), a glove with embedded sensors to track joint kinematics. The glove recorded flexion at the distal interphalangeal (DIP), proximal interphalangeal (PIP), and metacarpophalangeal (MCP) joints of the four fingers, and abduction (ABD) at the MCP joints, defined as movement away from a neutral position with fingers aligned and parallel. For the thumb, flexion at the MCP and interphalangeal (IP) joints, abduction at the carpometacarpal joint, and rotation (ROT) about the trapeziometacarpal joint axis were measured. In addition, palm arch (PA) and wrist (W) pitch and yaw were tracked. Subjects wore a CyberGlove on each hand during both experiments, but only data from the right hand, reported by all participants as dominant, are presented here. The glove sampled data at $\sim$200 Hz with a nominal angular resolution of $<0.1^{\circ}$.

In the Reach-and-Grasp Experiment, subjects began with their hands flat on a table. After three seconds of data collection, they were verbally instructed to grasp an object placed 30 cm in front of their hand. Each trial lasted 15 s and was repeated 20 times (4 trials per object for 5 objects). In the Manipulation Experiment, subjects began in the same starting position, with tools similarly placed 30 cm in front of them. After three seconds of data collection, they were instructed to begin a specific step of the wire harness assembly task. Data collection ended when subjects completed the task and returned their hands to the starting position. All subjects successfully completed the tasks using their right hand as the primary tool-using hand.

To detect movement onset, we calculated average joint velocity and smoothed it using a sliding window of five samples. Movement was identified when the smoothed displacement exceeded 5% of its maximum value across the data set. In the Reach-and-Grasp Experiment, the reach phase began at the first detected movement and ended at the last detected movement. The subsequent grasp phase concluded with the end of data collection. These phases were separated into two datasets: one containing the time-sampled measurements of 23 joint angles during reach, and the other during grasp. Each data set was further re-partitioned into 100 bins for analysis.

Following the approach of Mason et al. (14), we analyzed reach and grasp together. So, the two datasets were recombined to form the reach-and-grasp data of one subject during one trial; the reach-and-grasp phases were evenly weighted within the combined data set. In the Manipulation Experiment, data collection began after movement detection and continued until the step was completed. To account for the longer and variable durations of these steps, the data from each step was re-partitioned into 1,000 bins. This equal partitioning ensured that synergy extraction was not disproportionately influenced by steps of differing durations.

Data Analysis

Emergence of kinematic hand synergies.

To extract kinematic hand synergies, we used the singular value decomposition (SVD) method introduced by Mason et al. (14) to analyze the evolving hand postures in both tasks. In the Reach-and-Grasp Experiment, the data for each subject were organized into a matrix $X_{1,0}\epsilon R^{4,000\times 23}$, where columns represented 23 joint angles, and 4,000 rows stemmed from 200 bins $\times$ 5 objects $\times$ 4 trials. Similarly, in the Manipulation Experiment, we computed a matrix $X_{2,0}\epsilon R^{5,000\times 23}$, with rows representing 1,000 bins $\times$ 5 steps. Before applying SVD, data were centered by subtracting the mean of each column (55). Singular value decomposition computes the left and right singular vectors of a matrix. So, $\mathrm{SVD}(X_{i,j}) = U_{i,j}\Sigma_{i,j}V_{i,j}^{T}$ produces linear combinations of hand joint angles (i.e., kinematic synergies) in $V_{i,0}\epsilon R^{23\times 23}$, their temporal evolutions in $U_{1,0}\epsilon R^{4,000\times 4,000}\$$ or $U_{2,0}\epsilon R^{5,000\times 5,000}$, and an associated variance measure, the singular values, on the principal diagonal of $\Sigma_{1,0}\epsilon R^{4,000\times 23}$ or $\Sigma_{2,0}\epsilon R^{5,000\times 23}$.

While this analysis compared the Reach-and-Grasp and Manipulation Experiments as a whole, synergies may depend on object geometry (i.e., tool-specific). To address this, we conducted direct comparisons for specific tools. Data matrices were created for the reach-and-grasp of the zip tie, scissors, and screwdriver ($X_{1,1}$, $X_{1,2}$, $X_{1,3} \in R^{800\times 23}$) and their corresponding manipulation steps ($X_{2,1}$, $X_{2,2}$, $X_{2,3}$). As equal weighting of manipulation steps was unnecessary, joint position data were smoothed and downsampled to 60 Hz instead of partitioning into 1,000 bins. SVD was then applied to these matrices. Comparisons focused on the zip tie (*step 1*), scissors (*step 2*), and screwdriver (*step 3*); *steps 4* and *5* were excluded as they did not involve direct use of tools from the Reach-and-Grasp Experiment.

To measure the variance-accounted-for (VAF) by each kinematic hand synergy, we used the singular values from the diagonal of $\Sigma_{i,j}$. Specifically, VAF was calculated as the percentage of the square of a singular value relative to the total sum of squared singular values in $\Sigma_{i,j}$.

To determine whether manipulation and reach-and-grasp tasks can be described by the same number of synergies, we quantified the number of significant synergies following the method of Lambert-Shirzad and Van Der Loos (56). Significant synergies were defined as those required to achieve at least 90% VAF, with the addition of subsequent synergies contributing less than 5% additional VAF. To assess the effects of experiment and tool on the number of significant synergies, a 2 (experiment) × 4 (tool) repeated-measures ANOVA was performed.

Comparison of kinematic hand synergies.

Next, we assessed how well synergies from the reach-and-grasp task, commonly used to understand hand function (18), explain variance in the manipulation task. Specifically, we evaluated how the significant synergies identified in the reach-and-grasp task describe the manipulation data. Using singular value decomposition (SVD) as described previously, we first identified the significant synergies from the reach-and-grasp task, $V_{1,j}$. Next, to evaluate their explanatory power, we projected the centered manipulation data, $X_{2,j}$, onto the subspace defined by these significant reach-and-grasp synergies. This projection was computed as:

$$p_{2\ \mathrm{on}\ 1_j} = X_{2,j} \cdot V_{1,j}$$

where the subscript $p_{2\,\mathrm{on}\,1_j}$ denotes the projection of the manipulation data onto the reach-and-grasp synergies. For each projection, we calculated the variance of the manipulation data explained by these reach-and-grasp synergies:

$$var(p_{2\ \mathrm{on}\ 1_j}) = \frac{1}{n-1}\sum p_{2\ \mathrm{on}\ 1_j},$$

where n is the number of projections in $p_{2\ \mathrm{on}\ 1}$ (i.e., the number of data points).

The proportion of variance explained by these reach-and-grasp synergies was then calculated to assess how well they accounted for the manipulation task. This was done by dividing the sum of variance explained by the projection onto the significant reach-and-grasp synergies, $var(p_{2\ \mathrm{on}\ 1})$, by the sum of the eigenvalues of the manipulation synergies (i.e., the square of the diagonal values of $\Sigma_{2,j}$). Note that here we report the variance explained only by the significant reach-and-grasp synergies. This analysis provides insight into how much information about manipulation can be gleaned from the synergies identified in the simpler reach-and-grasp task.

Although the analysis aforementioned compared the size of the synergy space, it is also insightful to compare the form of the synergy space. Thus, we calculated the cosine similarities between the reach-and-grasp synergies, $V_{1,j}$, and manipulation synergies, $V_{2,j}$, for each subject. This involved computing the dot product of the two sets of synergies, resulting in a matrix, C_j, where each element $C_j(a, b)$ represents the cosine similarity between the ath reach-and-grasp synergy and the bth manipulation synergy. Here, we report the magnitude of these cosine similarities, ranging from 0 to 1.

$$C = \cos(\theta) = |V_1^T \cdot V_2|$$

If synergies were the same irrespective of experiment (i.e., the data span the same hyperspace), we would expect a matrix of cosine similarities, $C \in R^{m\times m}$, with ones on the diagonal and zeros otherwise. Conversely, if the reach-and-grasp synergies differed from the manipulation synergies (i.e., $V_1 \neq V_1$), the resulting cosine similarity matrix would be asymmetric. Specifically, $C(a, b) \neq C(b, a)$ as the element in $C(a, b)$ provides the cosine similarity between the ath reach-and-grasp synergy and the bth manipulation synergy while the element in $C(b, a)$ provides the cosine similarity between two different vectors, the bth reach-and-grasp synergy and the ath manipulation synergy. Additionally, in line with previous studies (57–60) we highlight cosine similarities greater than 0.9 as particularly significant. Moreover, the values along the diagonal of this matrix are referred to here as the synergy similitude—a measure of the degree of similarity between a subject's reach-and-grasp synergies, $V_{1,j}$, and their manipulation synergies, $V_{2,j}$.

Ideally, we would aim to test the hypothesis that two synergy vectors are identical, $V_{1,j} = V_{2,j}$, which would result in a cosine similarity of 1, $C(a, b) = 1$. However, cosine similarity is upper bounded by unity. Consequently, its distribution violates the implicit assumption of standard statistical test (i.e., approximate normality), eliminating our ability to statistically confirm equivalence.

Instead, to determine whether subjects' reach-and-grasp synergies differed from their manipulation synergies we tested the hypothesis that the two synergy vectors were orthogonal, $C(a, b) = 0$. To do so, we generated a null distribution by randomizing the order of the features in the manipulation synergy vector and computing the cosine similarity between the reach-and-grasp synergy and this randomized manipulation synergy. This process was repeated 1,000 times to create a distribution. We then calculated where the observed cosine similarity fell within this distribution. Notably, here we computed $C = \cos(\theta) = V_1^T \times V_2$, ranging from −1 to 1. Thus, the null distribution was centered around 0, with a standard deviation less than 1, which is important for hypothesis testing. Finally, the reported P value represents the probability of observing a cosine similarity as extreme as the actual value, assuming no relationship (i.e., orthogonal synergies $C(a, b) = 0$).

To assess whether synergy order affected synergy similitude (i.e., values along the diagonal of the cosine similarity matrix), we performed a linear regression between synergy order and similitude across all subjects. A significant effect was identified if the slope of the regression line differed significantly from zero (i.e., the 95% confidence interval of the slope did not include zero).

Recognizing that the default synergy order, based on variance-accounted-for, might be influenced by experimental noise, we reordered the manipulation synergies to optimize the analysis. Specifically, we reordered the columns of the manipulation synergy matrix, $V_{2,j}$, to maximize the sum of the diagonal values (i.e., similitude) in the cosine similarity matrix, C. Using this reordered matrix, we repeated the tests aforementioned to determine whether reach-and-grasp synergies differed from manipulation synergies and evaluated the effect of synergy order on similitude. Finally, we report the new rank of the manipulation synergies after re-ordering.

All analyses were conducted in MATLAB 2022b. Source data for this study are openly available at: https://github.com/michaelwestjr/wire-harnessing-experiment-data and https://doi.org/10.5281/zenodo.14532970.

RESULTS

Emergence of Kinematic Hand Synergies

Variance-accounted-for.

In general, manipulation required more synergies than reach-and-grasp. Figure 2 shows the average variance-accounted-for (VAF) by each synergy and their cumulative sum, while Fig. 3 illustrates the number of significant synergies for each tool and experiment. These values range from one synergy, in the case of one subject's reach-and-grasp of the screwdriver, to eight synergies, in the case of one subject's manipulation of the screwdriver. Despite this variability, fewer synergies were needed than the full 23 degrees of freedom (DOF) of the hand.

A two-way ANOVA (2 experiments × 4 tools) revealed significant main effects of experiment ($P = 1.07e$-10) and tool ($P = 3.9e$-06) on the number of significant synergies, and a significant interaction effect ($F_{3,48} = 18.86$, $P = 3.62e$-08).

Post hoc t tests showed that the number of significant synergies across all tools ($M = 5.43$, SD $= 0.76$) was greater than for the scissors ($M = 3.64$, SD $= 0.75$, $P = 2.73e$-06) and the screwdriver ($M = 4.34$, SD $= 2.44$, $P = 0.0051$). Similarly, the number of significant synergies for zip tie ($M = 4.86$, SD $=$ 1.66) was greater than for the scissors ($P = 0.0013$). Across experiments, manipulation ($M = 5.61$, SD $= 1.29$) required more significant synergies than reach-and-grasp ($M = 3.54$, SD $= 1.32$, $P = 8.7e$-13). Bonferroni-corrected comparisons ($\alpha_{\text{Bonferroni}} = 0.054/4 = 0.0125$) revealed that manipulation required more significant synergies than reach-and-grasp across all tools ($P = 8.93e$-04), the zip tie ($P = 5.14e$-04), and the screwdriver ($P = 4.44e$-07). However, no significant difference was observed for scissors ($P = 0.74$). To summarize, manipulation generally required higher degrees of freedom than reach-and-grasp, except in the case of scissors.

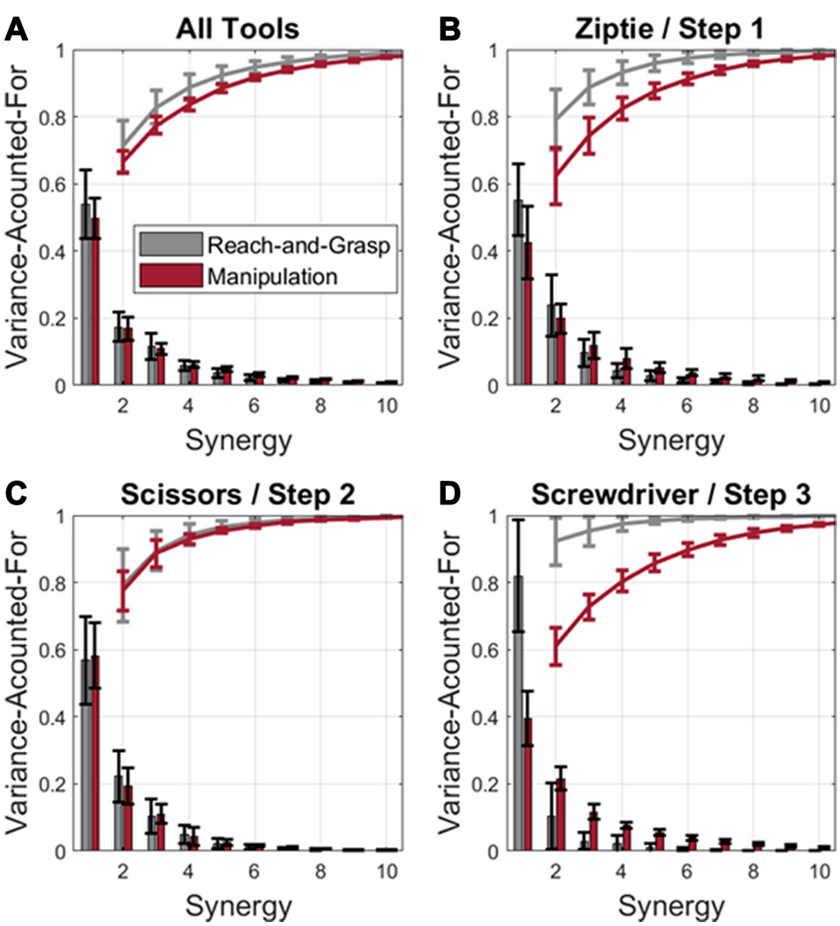

Figure 2. Variance-accounted-for (VAF) by each synergy averaged across subject for all tools (*A*), zip tie (*B*), scissors (*C*), and the screwdriver (*D*). Lines show the cumulative sum of the VAF. Error bars are ±1 standard deviation.

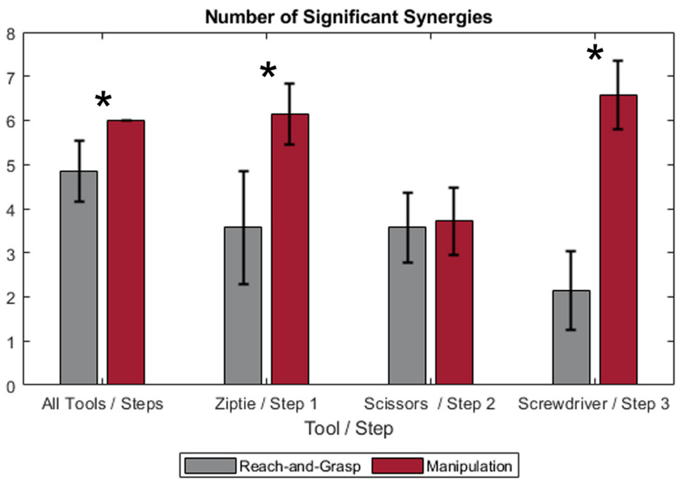

Figure 3. Number of significant synergies in reach-and-grasp or manipulation of each tool averaged across subjects. Error bars are ±1 standard deviation. *Significant difference between the number of reach-and-grasp and manipulation synergies.

Kinematic hand synergies.

As mentioned earlier, we used singular value decomposition to compute the synergies in our data set. The first reach-and-grasp and manipulation synergies computed for each subject are shown in Fig. 4 for the All Tools data set and in Supplemental Fig. S1 for the tool specific datasets. Across all datasets, the first synergy was dominated by flexion of the MCP and PIP joints, consistent with the power grasp described in prior studies (2, 12, 18). This motion was highly consistent across subjects. The second synergy, primarily characterized by thumb rotation (Fig. 4 and Supplemental Fig. S2), showed greater variability across subjects. For the third synergy (Fig. 4 and Supplemental Fig. S3) and higher-order synergies, substantial variation among subjects precluded the identification of a consistent physiological movement pattern.

Comparison of kinematic hand synergies.

Although Figs. 2 and 3 compare the size of the synergy subspaces, they do not address their form. To compare the form of synergies across the two experiments, we computed a cosine similarity matrix, with results shown in Supplemental Fig. S4. Each row represents a tool subset, and each column corresponds to a subject. The bottom row shows the average similarity matrix across all subjects. Values greater than 0.9 are highlighted for clarity. Specifically, in the "All Tools" data set, three of seven subjects exhibited a cosine similarity greater than 0.9 for the first synergy comparison. For scissors, two of seven subjects showed a cosine similarity greater than 0.9 for the first synergy, and one subject for the third synergy. No cosine similarities exceeding 0.9 were observed for the zip tie or screwdriver. Moreover, despite the evident

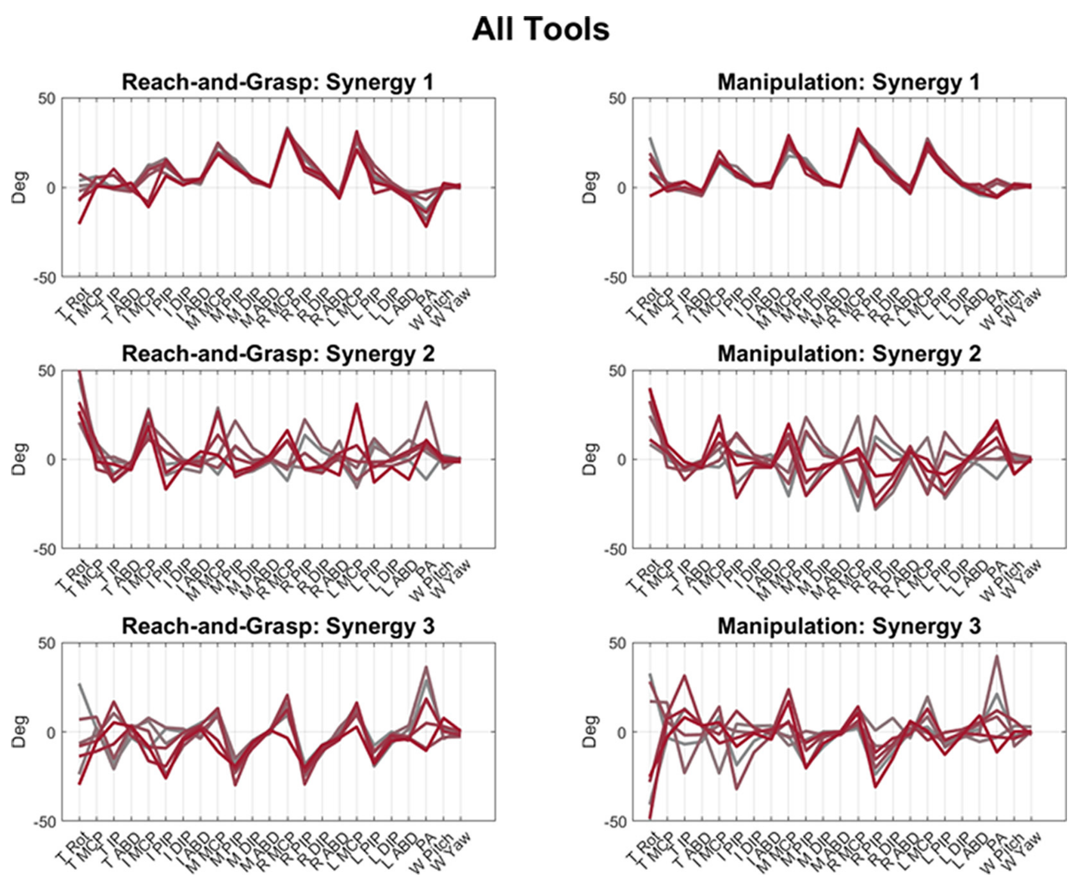

Figure 4. The first, second, and third synergy extracted using the all tools dataset. Each line denotes a different subject. Each row corresponds to synergy order, while each column denotes synergies computed across either reach-and-grasp, $V_{1,0}$, or manipulation, $V_{2,0}$. Note, the abbreviations T, I, M, R, and L refer to the thumb, index, middle, ring, and little fingers, respectively, while W refers to the wrist.

Table 1. *The number of statistically similar synergies upon comparing a subjects' reach-and-grasp synergy (syn) to their manipulation synergy (syn) of the same order*

	Number of Statistically Similar Synergies							
	Syn 1	Syn 2	Syn 3	Syn 4	Syn 5	Syn 6	Syn 7	Syn 8
All Tools	7	6	6	4	3	2	0	0
Zip tie/*Step 1*	5	3	3	3	1	1	0	0
Scissors/*Step 2*	5	4	5	2	0	0	0	0
Screwdriver/*Step 3*	6	1	3	0	2	3	0	0

The total number of subjects was 7. For brevity, only the first 8 synergies are shown. No subsequent synergies were statistically similar.

individual differences, the average across subjects reflects common features seen in all subjects: the first synergies between experiments exhibited higher similarity, whereas similarity decreased for higher-order synergies.

To test whether reach-and-grasp synergies differed significantly from manipulation synergies, we tested the null hypothesis, $C(a, b) = 0$, for each synergy pair. A rejection of this hypothesis indicates that the reach-and-grasp and manipulation synergies span a similar subspace. Table 1 summarizes the number of statistically similar synergy pairs of the same order across subjects, based on the diagonal of the cosine similarity matrix in Supplemental Fig. S4. As synergy order increased, the number of statistically similar synergies decreased, highlighting the divergence of higher-order synergies.

To assess the effect of synergy order on synergy similitude (i.e., the diagonal of the cosine similarity matrix), we performed a linear regression between synergy similarity and synergy order across all subjects, including only significant synergies (Fig. 3). The results are shown in Fig. 5. In all cases, the regression slopes were negative and significantly different from zero (All Tools: $P = 2.1e\text{-}07$; Zip tie/*step 1*: $P = 0.009$; Scissors/*step 2*: $P = 0.0055$; Screwdriver/*step 3*: $P = 0.0022$). Although the coefficients of determination were in the medium to low range (All Tools: $R^2 = 0.49$; Zip tie/*step 1*: $R^2 = 0.19$; Scissors/*step 2*: $R^2 = 0.27$; Screwdriver/*step 3*: $R^2 = 0.19$), all of the regression models were significant when compared with a constant model; hence, the significant slope. Thus, we conclude that synergy similarity decreased with synergy-order.

The default synergy order from SVD was based on the variance-accounted-for (VAF), with higher-order synergies explaining less variance. Although our similitude measure focused on cosine similarity between synergies of the same order, this approach did not ensure comparisons between the most similar synergies across reach-and-grasp and manipulation tasks. To address this, we reordered the manipulation synergies to maximize similitude with the reach-and-grasp synergies, as shown in Supplemental Fig. S5. After reordering, in the "All Tools" data set, three of seven subjects exhibited a cosine similarity greater than 0.9 for the first synergy. For scissors, two of seven subjects showed a similarity greater than 0.9 for the first synergy, and one subject for the third synergy. No similarities above 0.9 were observed for the zip tie or screwdriver. The number of statistically similar synergies is quantified in Table 2, where a higher incidence of similarity along the diagonal was observed compared with Table 1. This increase confirms that reordering improved the

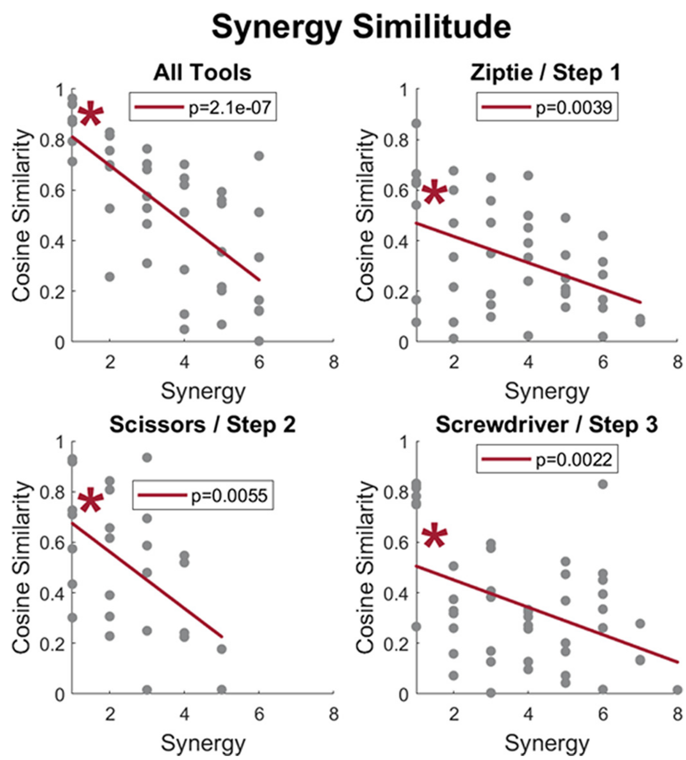

Figure 5. Synergy similitude (i.e., the diagonal of the cosine similarity matrix) across participants computed across each tool. *Significant slope.

alignment of reach-and-grasp and manipulation synergies, emphasizing their shared subspaces.

Figure 6 shows the synergy similitude after reordering the manipulation synergies. To assess the effect of the new synergy order on synergy similitude (i.e., the diagonal of the cosine similarity matrix), we performed a linear regression between synergy similarity and synergy order across all subjects, including only significant synergies. Unlike Fig. 5, negative regression slopes were significant only for the All Tools ($P = 1.0e\text{-}05$, $R^2 = 0.49$) and Screwdriver/*step 3* ($P = 1.7e\text{-}03$, $R^2 = 0.28$) datasets, but not for the Zip tie/*step 1* ($P = 0.05$, $R^2 = 0.09$) or Scissors/*step 2* ($P = 0.42$, $R^2 = 0.026$) datasets. Note, here the coefficient of determination of these linear regressions were in the medium range for the data whose model did present a significant slope and in the very low range, $R^2 < 0.1$, for the data whose model did not present a

Table 2. *The number of statistically similar synergies upon reordering the columns of the manipulation synergy (syn) matrix to maximize similitude (i.e., the diagonal of the cosine similarity matrix)*

	Number of Statistically Similar Synergies after Reordering							
	Syn 1	Syn 2	Syn 3	Syn 4	Syn 5	Syn 6	Syn 7	Syn 8
All Tools	7	7	7	6	7	5	0	0
Zip tie/*Step 1*	7	7	7	4	5	5	2	0
Scissors/*Step 2*	6	6	6	4	2	0	0	0
Screwdriver/*Step 3*	7	7	7	4	6	6	1	1

The total number of subjects was 7. For brevity, only the first 8 synergies are shown. No subsequent synergies were statistically similar.

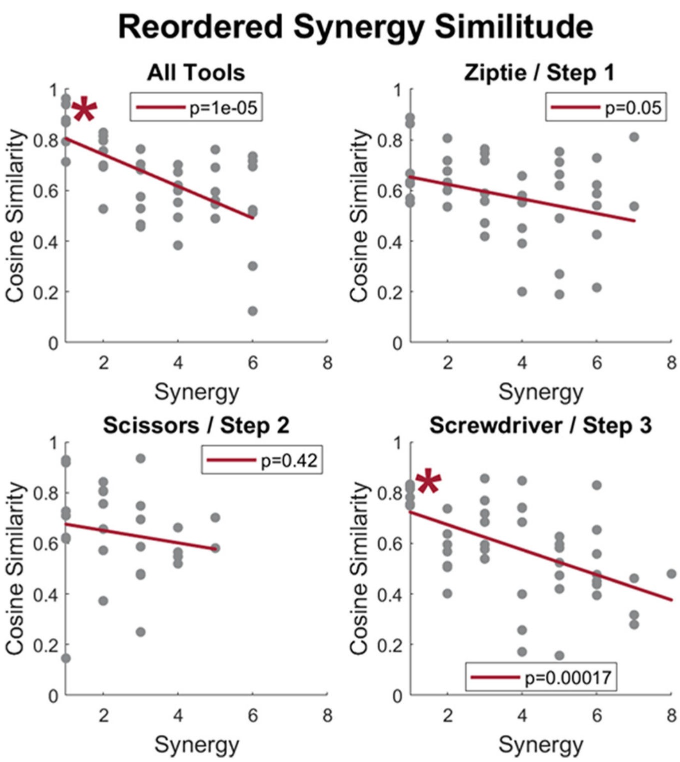

Figure 6. Synergy similitude (i.e., the diagonal of the cosine similarity matrix) across participants computed across each tool, upon reordering the columns of the manipulation synergy matrix to maximize similitude. *Significant slope.

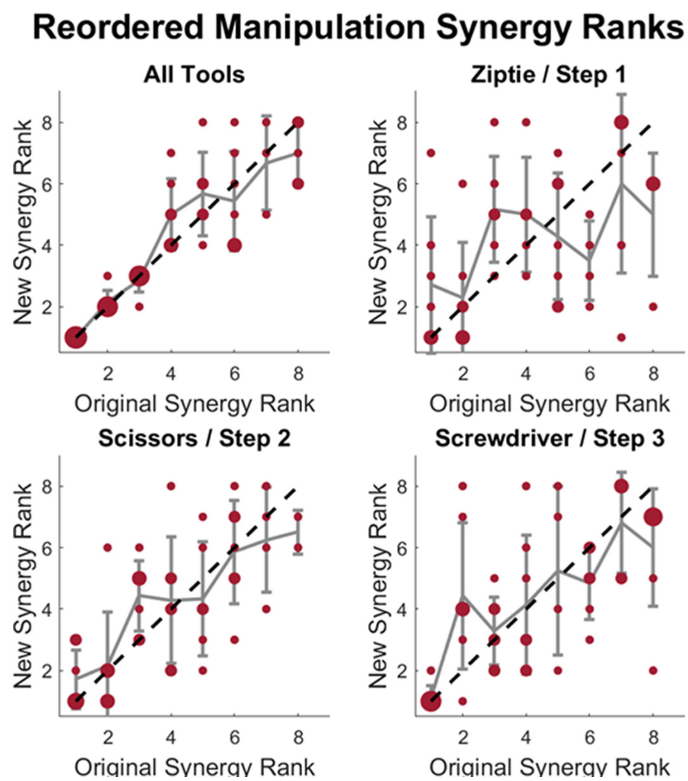

Figure 7. Manipulation synergy ranks after reordering to maximize similitude with the reach-and-grasp synergies (i.e., the diagonal of the cosine similarity matrix). The gray line represents the average, and error bars denote the standard deviation. Red dots indicate data points, with larger dots representing repeated values. The dashed black line indicates no change in rank; values above it suggest that synergies less dominant in reach-and-grasp became more dominant in manipulation, whereas values below it suggest the opposite.

significant slope. This may indicate that there was similarity between the reach-and-grasp and manipulation synergies, especially in the handling of the zip tie and scissors. However, in all tools and screwdriver data these results suggest that synergies clearly present in manipulation may not be as prevalent in reach-and-grasp.

Figure 7 illustrates how reordering the manipulation synergies increased the incidence of statistically similar synergies (Table 2). The dashed black line represents no change in synergy order after reordering. Synergies above this line decreased in rank, becoming more dominant in manipulation, whereas those below the line increased in rank, becoming less dominant. Notably, higher-order synergies often shifted to lower ranks (more dominant) in manipulation, whereas lower-order synergies shifted to higher ranks (less dominant), particularly in the screwdriver data set. This indicates that synergies considered insignificant in reach-and-grasp gained importance during manipulation tasks, highlighting the functional differences in synergy use between the two tasks.

Although informative, the cosine similarity analysis does not directly address how well the reach-to-grasp synergies explain the manipulation data. To explore this, we projected the manipulation data onto the significant reach-and-grasp synergies and calculated the variance they explained (VAF). Table 3 compares the VAF of manipulation data projected onto reach-and-grasp synergies with the VAF explained by the manipulation synergies themselves (values in parentheses). Across all subjects and tasks, the reach-and-grasp synergies consistently explained less variance in manipulation data, particularly in dexterous tasks like tying a zip tie or using a screwdriver. For instance, in *subject 4,* the reach-and-grasp synergies explained only 0.21 and 0.47 of the variance for the zip tie and screwdriver tasks, compared with 0.93 and 0.90 by the manipulation synergies. These findings suggest that while reach-and-grasp synergies can capture some aspects of manipulation, they fall short in tasks requiring fine

Table 3. *VAF by projecting the manipulation data onto the reach-and-grasp synergies, presented for all tools and specific tool-task pairings (Zip tie/Step 1, Scissors/Step 2, and Screwdriver/Step 3)*

VAF by Projecting the Manipulation Data onto the Reach-and-Grasp Synergies				
Subject	All Tools	Zip tie/ *Step 1*	Scissors/ *Step 2*	Screwdriver/ *Step 3*
1	0.81 (0.91)	0.49 (0.93)	0.61 (0.94)	0.34 (0.93)
2	0.80 (0.92)	0.60 (0.93)	0.81 (0.94)	0.47 (0.91)
3	0.81 (0.92)	0.76 (0.91)	0.84 (0.91)	0.27 (0.91)
4	0.78 (0.93)	0.21 (0.93)	0.79 (0.90)	0.47 (0.90)
5	0.86 (0.91)	0.62 (0.90)	0.78 (0.91)	0.35 (0.93)
6	0.70 (0.91)	0.40 (0.90)	0.66 (0.93)	0.48 (0.91)
7	0.73 (0.92)	0.75 (0.93)	0.74 (0.92)	0.67 (0.92)
Average	0.78 (0.92)	0.55 (0.92)	0.75 (0.92)	0.44 (0.92)

Values in parentheses indicate the VAF explained by the significant manipulation synergies themselves, as highlighted in Fig. 2 (red). VAF, variance accounted for.

motor control, highlighting the need to study more complex, functional manipulation tasks.

DISCUSSION

In this study, we tested two hypotheses: *1*) the number of synergies underlying manipulation is the same as those underlying reach-and-grasp, and *2*) the identity of synergies underlying manipulation is different from those underlying reach-and-grasp. We found that more synergies were required to competently describe the manipulation data than the reach-and-grasp data. Moreover, upon comparing the kinematic hand synergies across reach-and-grasp and manipulation, we found that the difference was predominantly in the higher-order synergies. After reordering the manipulation synergies to maximize similitude (i.e., the diagonal of the cosine similarity matrix), we found that synergies clearly present in manipulation may not be as prevalent in reach-and-grasp.

Emergence of Kinematic Hand Synergies

Our analysis did confirm a reduction of the hand's operational degrees of freedom. The first three synergies accounted for greater than 75% of the variance in both experimental tasks (Fig. 2). This value is consistent with what has been reported in prior literature (12, 14–16, 18) and cannot be explained solely by biomechanical constraints (15). Thus, we conclude that this simplified kinematic analysis can continue to be useful to understand aspects of motor control of the human hand performing a functional task and is not solely a function of biomechanics.

Consistent with much of the synergy work first introduced by Santello et al. (12), the first synergy, in both of the experimental tasks presented here, was dominated by flexion of the MCP and PIP joints (Fig. 4 and Supplemental Fig. S1). This power grasp synergy (2) has been observed across several experiments that studied hand posture in grasping, both with and without contact (13, 14); and even including signing in American sign language (16).

Our analysis confirmed a reduction in the hand's operational degrees of freedom in both experiments. However, more synergies were required to account for the same variance in the Manipulation Experiment than in the Reach-and-Grasp Experiment (Fig. 3), with statistically significant differences observed for all tools, the zip tie, and the screwdriver. Interestingly, this was not the case for the scissors, likely because the object's constraints limited finger and thumb motion, reducing variability. Since greater variability in motion typically increases the number of significant synergies, the constrained motion required by scissors likely explains the lack of a statistical difference between the number of significant synergies in reach-and-grasp and manipulation. We want to highlight that the intuitiveness of this result reassured us that despite the challenge of noisy data and complicated processing, our analysis did not detect differences when none were to be expected.

Unlike the scissors, in the other tools studied here, more synergies were required to account for the same variance in the Manipulation Experiment than in the Reach-and-Grasp Experiment (Fig. 3). For instance, using a screwdriver involves repeated gripping and turning motions, often requiring finger gaiting, whereas manipulating a zip tie demands fine-grained finger control rather than a simple power grasp (*synergy 1*). The greatest difference in synergies was observed for screwdriver tasks, which require multiple re-grasps and finger gaiting, followed by the zip tie. Together, these results suggest that a greater variety of hand postures was used when manipulating a tool or object than when reaching for and grasping it, unless that tool greatly constrained hand motion. This may be because manipulation requires more variable hand kinematics than reach-and-grasp, which also suggests that high-order synergies may be more important in manipulation than in reach-and-grasp. Intuitively, this would be consistent with the need for high dexterity in tasks that require object manipulation.

Reach-and-Grasp versus Manipulation Synergies

As reach-and-grasp synergies have historically informed prosthetic design and rehabilitation protocols, we set out to determine how well these synergies account for manipulation data. To address this, we projected manipulation data onto the significant reach-and-grasp synergies and calculated the variance they explained (Table 3). The results clearly demonstrate that the subspace defined by the reach-and-grasp synergies is not sufficient to describe the manipulation data. In all cases, the reach-and-grasp synergies accounted for significantly less variance in the manipulation tasks than the synergies derived directly from manipulation data. This discrepancy was particularly pronounced in fine manipulation tasks, such as tying a zip tie or using a screwdriver, which require complex and dexterous motions. These findings suggest that while reach-and-grasp synergies capture some essential aspects of hand function, they are insufficient to fully describe the more intricate demands of manipulation. This understanding is crucial for two key reasons. First, it highlights the importance of studying manipulation tasks that require fine dexterity to inform rehabilitation protocols. This will help ensure that future rehabilitation protocols are functionally relevant and tailored to real-world activities. Second, further study of the dissimilarities between the manipulation and reach-and-grasp spaces can inform the development of robotic control algorithms aimed at replicating human dexterity (28, 46). Ultimately, understanding these nuanced differences between the subspaces of control for manipulation tasks and reach-and-grasp can both help improve rehabilitation protocols aimed at restoring hand function and decrease the gap between human and robot dexterity.

With this in mind, we aimed to directly compare the synergies between reach-and-grasp and manipulation tasks (Supplemental Fig. S4), focusing on the diagonal values of the similarity matrices—the synergy similitudes. As shown in Fig. 5, synergy similarity decreased with increasing synergy order. These differences in higher-order synergies between reach-and-grasp and manipulation tasks suggest that current knowledge of higher-order kinematic synergies may not reliably apply to functional tasks. Given that higher-order synergies become significant during manipulation (Fig. 3), further investigation of these differences is essential.

It is important to note that higher-order synergies are often dismissed because they do not explain a significant portion of the variance in the data, and their minimal contribution is typically considered indistinguishable from noise (i.e., they are near the "noise floor"). In our data, the first synergy consistently represented a power grasp, whereas higher-order synergies showed significant differences between reach-and-grasp and manipulation tasks. Often overlooked as experimental error or noise, these synergies can obscure critical distinctions between reach-and-grasp and manipulation. Our findings align with the study by Yan et al. (61), who demonstrated that low-variance principal components exhibit structured, condition-specific variations rather than mere noise. Here, we align with their assertion that higher-order synergies can provide critical insights into the complexities of human motor control. In this study, we have elucidated these distinctions by refraining from dismissing higher-order synergies.

Investigating the diagonal values of the similarity matrices in Supplemental Fig. S4 assumes that synergies of the same order are identical, though this need not be the case. In fact, in Supplemental Fig. S4, several off-diagonal comparisons show statistically similar synergies. To better assess similarity between reach-and-grasp and manipulation synergies and address potential concerns about spurious rankings, we reordered the manipulation synergies in Supplemental Fig. S5 to maximize diagonal cosine similarities (Fig. 6), resulting in an increased incidence of statistically similar synergies on the diagonal (Table 2). Figure 7 shows that higher-order manipulation synergies often shifted in rank—becoming more significant—whereas lower-order synergies became less important, especially in screwdriver use. This reflects the shift in functional demands: grasping a screwdriver involves a power grasp (*synergy 1*), whereas using it requires tool rotation and finger-gaiting motions, emphasizing higher-order synergies. These findings highlight the importance of typically overlooked higher-order reach-and-grasp synergies, which, despite being near the "noise floor," play a critical role in manipulation.

Limitations

Because the manipulation experiment inherently included a reach component, it was not possible to completely decouple the two groups of synergies. Although reach data contributed to both groups, the reach portion of the first experiment averaged 4.75 s, compared with 92.73 s for the full manipulation trials. Thus, the synergies derived from the manipulation data were minimally influenced by the reach motion. Nonetheless, our results showed clear differences between the reach-and-grasp and manipulation synergies; inclusion of reach would make the synergies more similar, not more distinct.

Singular value decomposition was used to extract the kinematic hand synergies. This is only one of many dimensionality reduction techniques and suffers flaws; however, it is the most commonly used in kinematic data (18). As a data-driven approach, it is susceptible to data preprocessing effects. We aimed to mitigate this by following the guidelines presented by West et al. (55). Namely, we centered the data by removing the mean; this ensured that we did not obtain a dominant first synergy that only served to center the data and thereby reduced the number of significant synergies (55). Moreover, we chose to bin the data in a manner that was least likely to change the variance within the data; doing so would have resulted in a synergy indicating related DOFs but without accurate quantification of their co-variation (55). Although it is possible that our results may have been influenced by the data preprocessing and processing methods, reasonable assumptions consistent with prior literature were made in the synergy extraction methods.

Our goal was to test the hypothesis that two synergy vectors were the same, $V_{1,j} = V_{2,j}$. To compare reach-and-grasp and manipulation synergies, we calculated their cosine similarity, a metric ranging from -1 to 1. Since synergies with a cosine similarity of -1 or 1 span the same subspace, we reported the magnitude of the cosine similarity, ranging from 0 to 1. However, because cosine similarity is bounded by unity, its distribution violates the assumption of normality required for standard statistical tests. Therefore, we tested the null hypothesis that the two synergy vectors were orthogonal, $C_{i,j} = 0$. It is important to emphasize that falsification of this hypothesis strictly tells us that the two compared synergy vectors do not span completely orthogonal subspaces. Thus, the reported similar synergies in Tables 1 and 2 do not necessarily span the same subspace; rather, they do not span orthogonal subspaces. Due to these limitations, we cannot statistically confirm whether the compared vectors are equal. Thus, in line with other literature (57–60), the authors have highlighted cosine similarity greater than 0.9.

In this study, muscle dynamics and muscle synergies were not studied. As muscles are the human's actuators, one could argue that we cannot draw conclusions about the human motor controller. However, considerable insight has been gained from studying purely kinematic hand motion (12–16, 18, 27, 62–68). Moreover, studies of adaptation to visual and/or mechanical perturbation have shown that kinematics dominate human motion planning (69, 70). Studying muscle dynamics during manipulation is important and should be pursued further; however, one should not ignore the insights that can be gained from kinematics.

In the literature, a persistent question remains regarding the neural basis of synergies: are synergies the result of physical constraints and biomechanics, or are they a product of neuromotor control strategies? This question is critical to determine whether synergies serve as a simplifying control technique in motor coordination (18, 71–73). In this study, we analyzed kinematic variance across two tasks but did not explicitly separate "good" variance—variation that does not affect task performance—from "bad" variance, which does (74). This limitation may influence synergy interpretation, as our analysis did not account for constraints imposed by tools or the external environment. A more refined approach could involve projecting measured variations onto the tangent surface of these constraints, isolating intrinsic motor control strategies from extrinsic task-specific influences. For instance, if a subject is required to slide their fingertip along a surface, the surface's shape would impact the recorded finger kinematics and resultant singular value distribution. However, projecting the measured variation onto the plane tangent to the constraint could yield a better estimate of intrinsic motor control strategies, isolating them from extrinsic task-specific adaptations. Similar work by Sharma (75) provides a foundation for such methods, which could be extended to the functional manipulation tasks studied here. Future research should develop analytical techniques to account for these factors, improving synergy analysis in complex, constrained manipulation tasks.

Implications

Synergies have been used as a basis for rehabilitation post cerebral vascular accident (76–80) and have informed the design of several rehabilitation devices (76, 81–84). Although it may seem intuitive that more and distinct synergies are required for manipulation than for reach-and-grasp, many rehabilitation efforts have traditionally focused on grasp synergies for functional recovery. This study highlights the critical distinction between synergies for reach-and-grasp and those for manipulation, underscoring the need to design rehabilitation tasks that address the demands of tool-use and daily activities. For upper limb reaching, the advancement of robotic rehabilitation techniques has demonstrated greater effectiveness and better cost efficiency than standard patient care (85–88), largely due to insights into innate human motor function, as explored here. Ultimately, if we want to restore hand function to those who have lost it, kinematic hand synergies can be useful; however, they must be studied in the context of activities of daily living, which often require functional tool-use.

The results also have important implications for prosthetic design. Many prostheses simplify design by leveraging lower-order grasp synergies (18, 89–95). However, this study highlights the significance of higher-order synergies for tool-use, emphasizing the need to account for these distinctions in prosthetic design. Reliance solely on low-order synergies may fail to capture the full range of movements required for functional tool-use.

Are synergies an epiphenomenon?

The concept of synergies has a venerable history in the motor neuroscience and robotics literatures [for review see Santello et al. (18)]. Confining attention to kinematic synergies, as described earlier they may be defined by a time-invariant map $\phi(\cdot)$from a lower-dimensional control input $\delta \epsilon R^m$ to a higher-dimensional configuration space $\theta \in R^n$, where $n > m$, such that $\theta(t) = \phi(\delta(t))$. Numerical methods such as singular value decomposition may be applied to experimental data to identify a linear approximation to the map $\phi(\cdot)$. Is this concept insightful?

For example, any single action necessarily follows a path $p(\cdot)$ in configuration space. A highly skilled or well-learned action is likely to be repeatable such that every replication of the action follows the same path in configuration space. That path defines the coordinate of a one-dimensional (albeit likely nonlinear) subspace to which the task is confined. Displacement along that path $s \epsilon R^1$ defines a single coordinate. Its time-history $s(t)$ may serve as a control input to define the configuration-space trajectory $\theta(t) = p(s(t))$ used for the task. Therefore $p(\cdot)$ defines a synergy. By this reasoning, synergies are a necessary consequence of skill.

Moreover, distinct actions likely follow distinct paths $q(\cdot)$, $r(\cdot)$ etc. and each of these also defines a synergy. As a result, we may predict that synergies will vary with subject, task, and object, consistent with our findings and those of previous researchers (12, 13, 16, 17, 67). Thus, we may conclude that the dimensionality of a single highly learned action should be one. Imperfect execution or noise might lead to an apparent dimensionality greater than one. Those additional dimensions may be useful, for example, to absorb inevitable motor variability, but any additional dimensions do not describe the task.

Moreover, the linearization implicit in the use of numerical methods such as singular value decomposition may also lead to an apparent dimensionality greater than one. This may motivate the application of nonlinear approaches in future work.

Nonetheless, this reasoning does not challenge the biological reality of synergies. Learning a skill is loosely analogous to solving an optimization problem and is costly in time and physical and mental effort. Storing, and retrieving, learned patterns in the form of synergies may be a way to avoid the need to re-optimize on every execution. But there's no free lunch: we should expect that learning a task that requires a configuration-space path orthogonal to $p(\cdot)$, $q(\cdot)$, $r(\cdot)$ etc. will be much harder than learning a task that interpolates between these subspaces. That, too, has been reported (73, 96, 97).

A collection of skilled behaviors need not use all regions of configuration space but may be confined to a subspace spanned by the synergies $p(\cdot)$, $q(\cdot)$, $r(\cdot)$ etc. The key to identifying this skilled subspace is to study tasks that require the true versatility of human manipulation—such as wire-harnessing.

Conclusions

This study sought evidence of kinematic hand synergies during wire harness installation—a task that involves manipulation of complex tools and objects. Human hand motion was measured during two experiments: *1*) reaching for and grasping a tool or object and *2*) manipulating those objects. In both experiments, a reduction of the operational degrees of freedom was observed (i.e., synergies). Moreover, we found that manipulation of a tool generally required more significant synergies than grasp of that same tool. Nonetheless, consistent with previous literature on kinematic hand synergies, the first synergy participated in power grasp, and the second synergy was dominated by thumb rotation. However, upon comparing reach-and-grasp with manipulation, we found that synergy similarity decreased with synergy-order. Considering that higher-order synergies become significant during manipulation, it is important that we investigate these differences; this study serves as a point of entry to understanding them. Investigation of the human hand during functional object manipulation may lead to better prosthetic hand design, and hand rehabilitation techniques. If we want to restore hand function to those who have lost it we must study hand manipulation beyond grasping.

DATA AVAILABILITY

Source data for this study are openly available at: https://github.com/michaelwestjr/wire-harnessing-experiment-data.

SUPPLEMENTAL MATERIAL

Supplemental Figs. S1–S5: https://doi.org/10.5281/zenodo.14532970.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

A.M.W. and N.H. conceived and designed research; A.M.W. performed experiments; A.M.W. analyzed data; A.M.W. and N.H. interpreted results of experiments; A.M.W. prepared figures; A.M.W. drafted manuscript; A.M.W. and N.H. edited and revised manuscript; A.M.W. and N.H. approved final version of manuscript.

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