UNEXPECTED COMPLEXITY OF EVERYDAY MANUAL BEHAVIORS

Yuke Yan[1], James G. Goodman[1], Dalton D. Moore[1], & Sliman J. Bensmaia[1,2]

[1]Committee on Computational Neuroscience, University of Chicago, Chicago, IL
[2]Department of Organismal Biology and Anatomy, University of Chicago, Chicago, IL

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ABSTRACT

How does the brain control an effector as complex and versatile as the hand? One possibility is that the neural control of the hand is simplified by limiting the number of achievable hand postures. Indeed, hand kinematics can be largely accounted for within a small subspace. This oft replicated finding has been interpreted as evidence that hand postures are confined to this subspace and that leaving it volitionally is impossible. A prediction from this hypothesis is that measured hand movements that fall outside of this subspace reflect motor or measurement noise. To address this question, we track hand postures of human participants as they perform three tasks – grasping, typing, and signing in American Sign Language. We then apply a standard dimensionality reduction technique – principal components analysis – and replicate the finding that hand movements can be largely described within a much reduced subspace. However, we show that postural dimensions that fall outside of this subspace are highly structured and task dependent, suggesting that they too are under volitional control. We conclude that hand control occupies a high dimensional space and propose that the complexity of hand movements is well within the scope of the brain's computational power.

INTRODUCTION

From picking up a coffee cup to playing the piano, humans can engage in a wide range of manual behaviors, highlighting the staggering flexibility of the hand: The 27 bones and 39 muscles give rise to more than 20 degrees of freedom (DOF) of movement [1,2]. This versatility is also mediated by a sophisticated neural system: the hand is one of the most densely innervated regions of the human body [3] and the hand representation in sensorimotor cortex is disproportionately large [4]. Additionally, although primate motor cortex lacks a clear somatotopic organization [5], it nonetheless seems to contain a specialized module for hand control [6].

The complexity of the hand has called into question whether the central nervous system (CNS) can fluidly control such a complex effector [7,8]. An appealing hypothesis is that hand postures – which in theory can exist over 20 or more degrees of freedom – are reduced to a lower dimensional manifold to simplify the control problem [7–9]. Instead of spanning the space afforded by every DOF, hand control relies on a set of synergies that are combined to give rise to manual behaviors. Broadly defined, a synergy is a set of muscle activations or joint movements that are recruited in tandem, rather than individually [10]. This restriction of volitional movements of the hand to combinations of a small number of synergies would then help the CNS achieve fluid manual behaviors. To date, many studies have looked for hand synergies in different movement contexts, with a mixture of evidence for and against the notion that the CNS indeed constrains hand movements to a limited basis set [9–18].

The most compelling evidence for synergies stems from analysis of hand kinematics or of the muscle activations that drive them, which seem to occupy a lower dimensional manifold than might be expected from counting the DOFs. Indeed, principal component analysis (PCA) of kinematics or muscle activations reveals that a small number of principal components (PCs) account for most of the variance in the movements or activations, typically measured for a single behavior (e.g. grasping, playing piano, typing)[11,12,19–23]. The more or less explicit assumption underlying the interpretation of this dimensionality reduction is that high-variance principal components (PCs) – the synergies – are under volitional control whereas low-variance PCs reflect motor or measurement noise. Another possibility, however, is that the exquisite control of the hand is mediated by high dimensional sensorimotor signals, and that low-variance PCs are critical to achieving precise hand postures.

The aim of the present study is to assess whether hand movements exist in a manifold whose dimensionality is lower than its theoretical value, defined by the hand's DOFs. To this end, we have human participants perform three manual behaviors – grasping, signing letters in American Sign Language, and typing on a keyboard – while we track their hand kinematics. We then assess the degree to which low-variance PCs are structured by assessing the degree to which they carry information about the manual behavior. For example, humans and non-human primates precisely preshape their hands when grasping objects. Objects can thus be classified on the basis of the kinematics they evoke during grasping even before contact. If low-variance PCs indeed reflect noise, they should bear no systematic relationship with the object to be grasped. However, if low-variance PCs reflect subtle but volitionally controlled adjustments of hand posture to better preshape to the object, these should also be highly object specific. We also investigate the degree to which the space of hand movements depends on the behavior. Specifically, how similar are the kinematic spaces in the three manual behaviors?

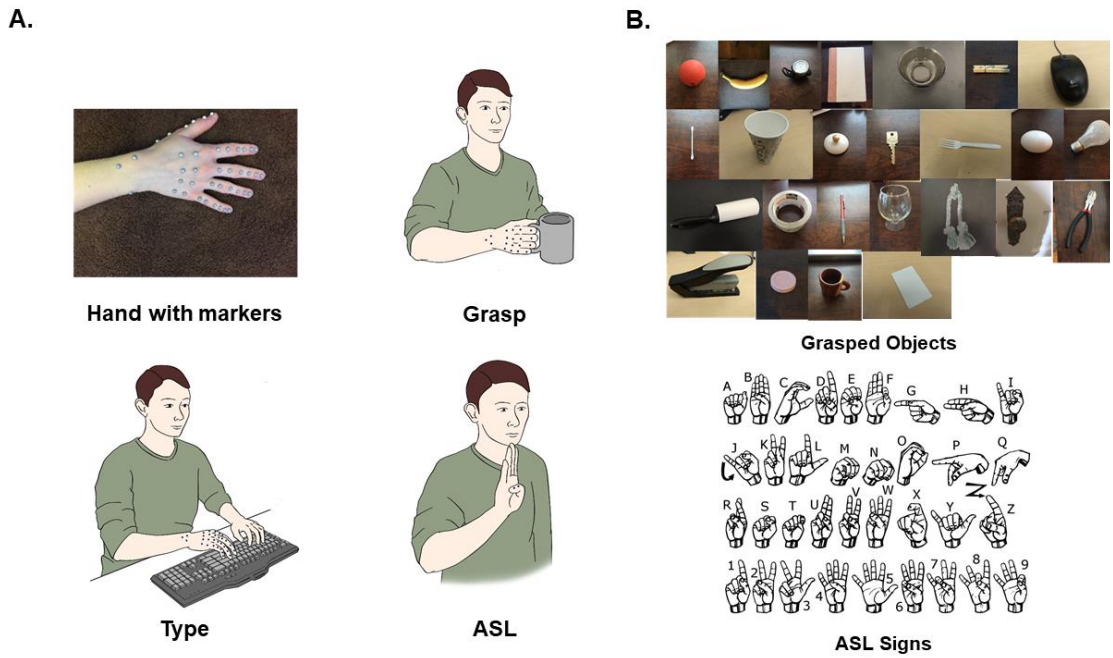

Figure 1. Experimental design. A| Subjects performed three different manual tasks with reflective markers placed on their right hand: Grasping objects, signing in American Sign Language, and typing on keyboard. Infrared cameras tracked the 3D trajectories of the markers and joint angles were calculated from them. B| Grasped objects and ASL signs.

METHODS

Hand kinematics

Experimental design

All procedures were approved by the institutional review board (IRB) of the University of Chicago. Eight right-handed adult subjects between the ages of 21 to 40 participated in the experiment. During the experiment, subjects were instructed to perform three different types of manual tasks: Grasping objects, typing on a keyboard, and singing letters in American Sign Language (ASL) (**Figure 1A)**. All eight subject performed the grasping and typing tasks and three subjects – who had prior knowledge of ASL

– performed the signing task. Grasping and ASL involved only the subjects' right hand and only the right hand was tracked during typing.

In the grasping tasks, subjects began each trial by resting their right hand on a table in front of them. The experimenter then placed an object at the center of the table and subjects grasped the object with their right hands, lifted it, and held it up for approximately 1 second before replacing the object on the table and moving their hand back to the starting position. This procedure was repeated five times for each object. Twenty five objects, varying in size, shape, and orientation were used to elicit 30 distinct grasps (some objects could be grasped in several ways; for example, a light bulb can be grasped by the stem or by the bulb, **Figure 1B**).

In the typing task, subjects used a keyboard to type two 300-word passages, each divided into four paragraphs of approximately equal length (**Supplementary Figure 3**). The first passage was a "word salad" designed to maximize right hand movements: All words were anagrams of the letters to the right of the "Y-G-V" boundary (inclusive) on a QWERTY keyboard. The words were arranged in written English syntax with common punctuations but did not follow any grammatical rules or carry any meaning. The second passage, taken from the Wikipedia page of neocortex (https://en.wikipedia.org/wiki/Neocortex), comprised approximately equal distributions of letters on both halves of the keyboard.

In the ASL task subjects started at the same position as in the grasping task. On each trial, subjects signed an ASL sign – one of the 26 letters of the alphabet or a number from 1 to 10 – and repeated it five times.

Measurement and pre-processing

Forty one infrared-reflective markers (hemisphere shape, 4-mm diameter) were placed on the right hand of each subject, with two markers covering each finger joint, two on the ulnar and one on the radial bone of the forearm (**Figure 1A**). Fourteen infrared cameras (8MP resolution, 250Hz) (MX-T Series, VICON, Los Angeles, CA) fixed to wall mounts and camera stands tracked the 3D trajectories of each marker, each of which was then labeled based on its respective joint using Vicon Nexus Software (VICON, Los Angeles, CA). We then calculated inverse kinematics using time-varying marker positions and a musculoskeletal model of the human arm (https://simtk.org/projects/ulb_project) [24–30] implemented in Opensim (https://simtk.org/frs/index.php?group_id=91) [31]. The model was modified to include three rotational degrees of freedom of the first and fifth carpo-metacarpal joints to permit reconstructions of oppositional movements of these digits. In total, we reconstructed the time-varying angles of 29 degrees of freedom, including all movement parameters of the hand and three of the wrist.

Analysis

Principal components analysis & cross-projection similarity

Kinematic synergies have been identified using principal components analysis (PCA), which expresses hand postural trajectories in terms of a set of orthogonal bases, each of which consists of correlated joint trajectories. We applied PCA to the hand kinematics obtained from each individual subject [32]. To compare PC subspaces across subjects or tasks, we computed the cross-projection similarity [11]. For this, we first calculated the total variance accounted for by the first N PCs of one group (V1). Then, we projected the scores of the first N PCs of that group onto the first N PCs of a second group and

computed the total variance explained in group 1 by the projection onto group 2 PCs (V2). Finally, we computed the ratio V2/V1. The ratio V2/V1 approaches 1 to the extent that the second subspace resembles the first. To compare kinematic subspaces across tasks, we performed a PCA on the data from each task pooled across subjects and computed the cross-projection similarity using the first 10 PCs (~95% variance explained).

Classification

Next, we assessed the degree to which hand kinematics were condition-specific. That is, we gauged the extent to which hand postures were dependent on the object to be grasped or the letter/number to be signed. To this end, we used linear discriminant analysis (LDA) to classify conditions based on the instantaneous hand posture (measured in joint angles) 100-ms before object contact or when the ASL sign had been achieved. Classification performance with the full kinematics provided a ceiling of the achievable classification with LDA.

Next, we gradually removed PCs in descending order of variance by reconstructing the hand posture on each trial based on a progressively smaller subset of PCs. We then used LDA to classify the grasped object or the ASL posture with leave-one-out cross validation. That is, we trained a linear discriminant classifier with the reconstructed hand postures from N-1 randomly selected trials (where N is the total number of trials) and used it to classify the final trial, leaving out each trial on successive iterations. Performance was gauged by the proportion of correct classifications.

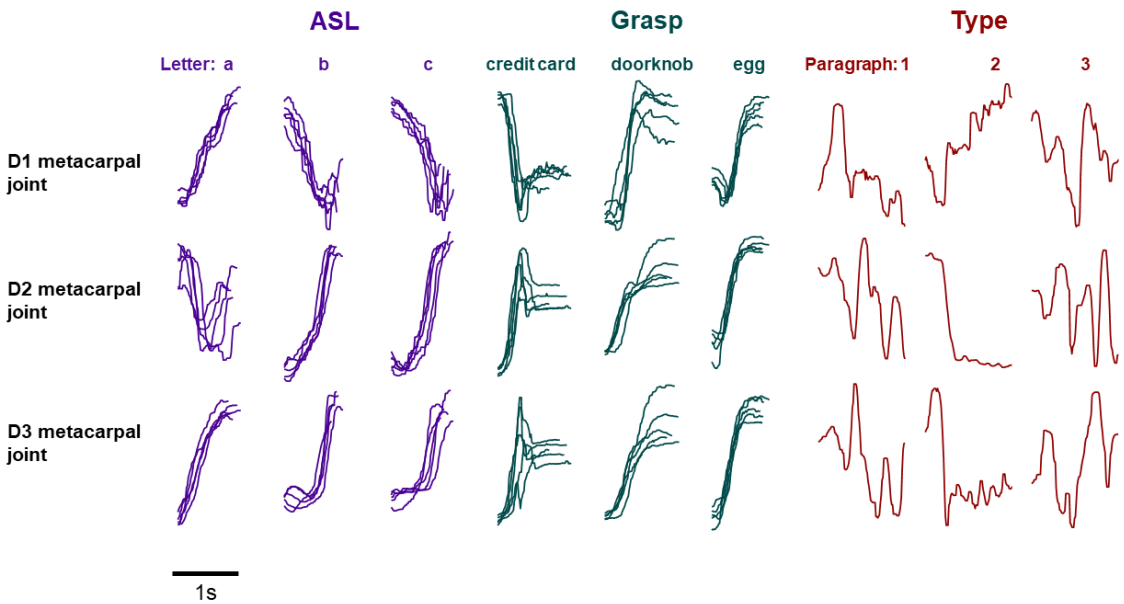

Figure 2. Example kinematic traces. Joint kinematics (metacarpophalangeal joints flexion of digits 1 to 3) evoked during the three manual tasks: ASL, grasp and typing. For ASL and grasp, the kinematics evoked during grasping of three different objects or signing of three ASL signs are shown for five trials. For typing, the initial 1-second epoch of typing three different paragraphs is shown.

RESULTS

Subjects performed three tasks – grasping various objects, signing the letters of the alphabet in American Sign Language (ASL), and typing two paragraphs on a computer keyboard – while we tracked their hand movements using a camera-based motion tracking system. We wished to examine the degree to which the structure of hand movements was task dependent and differed across individuals. We also wished to ascertain the degree to which hand movements occupy a low-dimensional manifold.

As might be expected, different joint trajectories were observed when subjects grasped different objects or signed different ASL letters (**Figure 2**). Moreover, the kinematics were consistent within condition – grasping a specific object of signing a specific letter – as evidenced by similar trajectories over repeated presentations of the same condition.

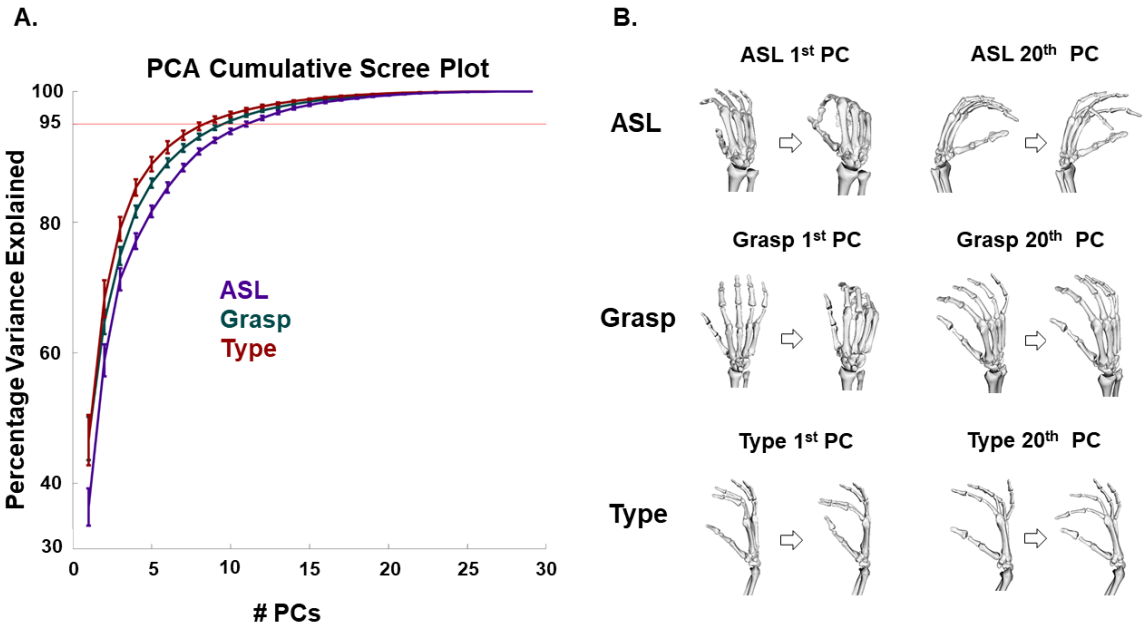

Figure 3. Principal component analysis. A| Cumulative variance plot showing the total percentage of variance explained vs. the number of principal components. PCA is performed separately for each task and subject. The curves are averaged across 8 subjects for grasp and typing and 3 subjects for ASL. B| Visualization of example PCs. For each task, we show the 1st and the 20th PCs (in terms of variance explained). The 20th PC accounts for less than one percent of the variance.

Structure of hand kinematics for three manual tasks in humans

First, we wished to reproduce previous findings that much of hand kinematics can be described within a lower dimensional subspace. To this end, we performed a PCA on the joint angles and examined the cumulative variance plot. We found that 3-5 PCs were sufficient to account for 80% of the variance in the kinematics and 8-11 principal components (PCs) accounted for 95% of variance, consistent with previous findings (**Figure 3A**)[12,33]. We then examined PCs with large and small eigenvalues (**Figure 3B**). In line with previous findings, the first two PCs of grasp and ASL involved opening and closing the hand, engaging mostly metacarpophalangeal (MCP) joint flexion/extension, some proximal and distal interphaleangeal joint flexion/extension (PIP and DIP), and some wrist flexion. One might expect PCs with small eigenvalues to reflect motor or measurement noise and thus be unstructured. Instead,

examination of low-variance PCs (the 20th, e.g.) revealed coordinated joint movements (e.g. ring PIP and MCP flexion in ASL, "pinch" flexion in type) that were systematically dependent on condition (**Figure 3B**).

Task- and subject-dependence of the kinematic structure

Next, we compared the subspace of hand kinematics across tasks. To this end, we used a cross-projection similarity measure which gauges the extent to which PCs derived from the kinematics in one task account for the kinematics in the other, and vice-versa [11]. We found that the PC subspaces of all three tasks were more similar than would be expected by chance (two-sample t-test, DOF = 210, p = 9.29e-110) and that the kinematic subspaces of ASL and Grasp were similar but differed from the kinematic subspace of typing (two-sample t-test, DOF = 110, *p* =2.58e-05) (**Figure 4A**). We then gauged the degree to which the kinematic subspaces were similar across subjects using the same similarity measure and found that PC subspaces from the same task but different subjects were more similar to each other than were PC subspaces from the same subject but different tasks (paired t-test, *DOF = 56*, *p* = 1.65e-05) (**Figure 4B**). That is, different tasks involve different kinematic structure but that structure is consistent across individuals (cf. [34]).

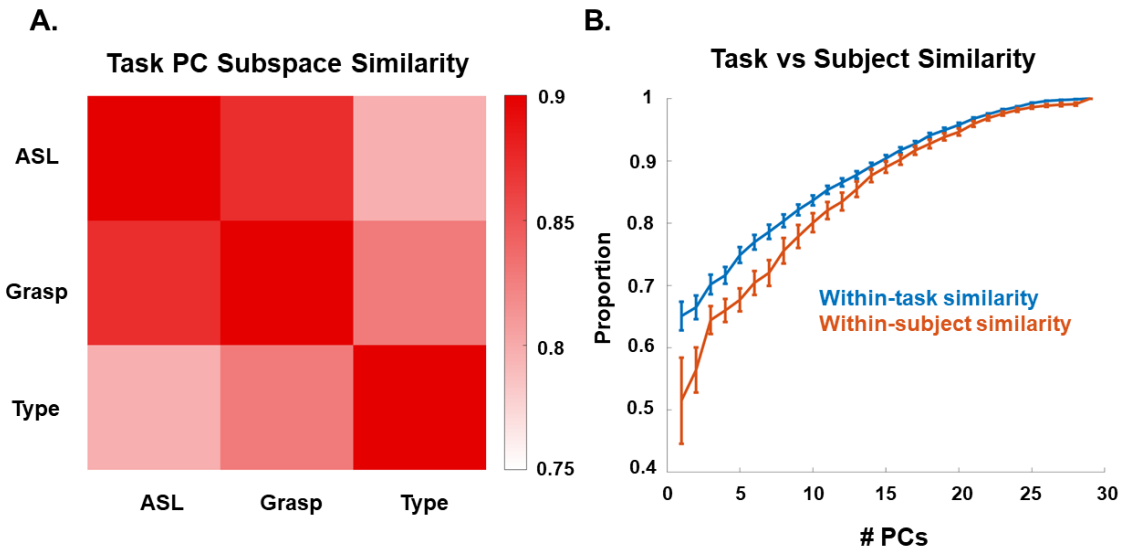

Figure 4. Similarity of kinematic manifolds across tasks and subjects. A| Similarity of the subspaces (formed by the first 10 PCs, accounting for 95% Variance) of pairs of tasks, gauged by cross-projection similarity [36]. ASL and grasp occupy similar manifolds and typing is distinct from these. B| Mean subspace similarity within task/across subjects and the converse. Differences in kinematic manifolds are more pronounced across tasks than they are across subjects.

Structure of low-variance PCs

Having replicated previous results that (1) hand movements can be reconstructed with high precision using a reduced basis set and (2) the resulting synergies are consistent across subjects, we then examined whether the low-variance PCs were structured. We found that the kinematics projected on the low-variance PCs across repeated presentations of the same condition (same grasped object, same ASL letter) varied systematically with the grasped object or signed letter (**Figure 5 A, B**), although this structure was noisier than that in the high-variance PCs, as might be expected (**Figure 5 C, D**). In other words, even the low-variance PCs reflect structure rather than noise in the kinematics. The trajectories along all PCs were far more consistent than would be expected by chance (See **Figure S1**).

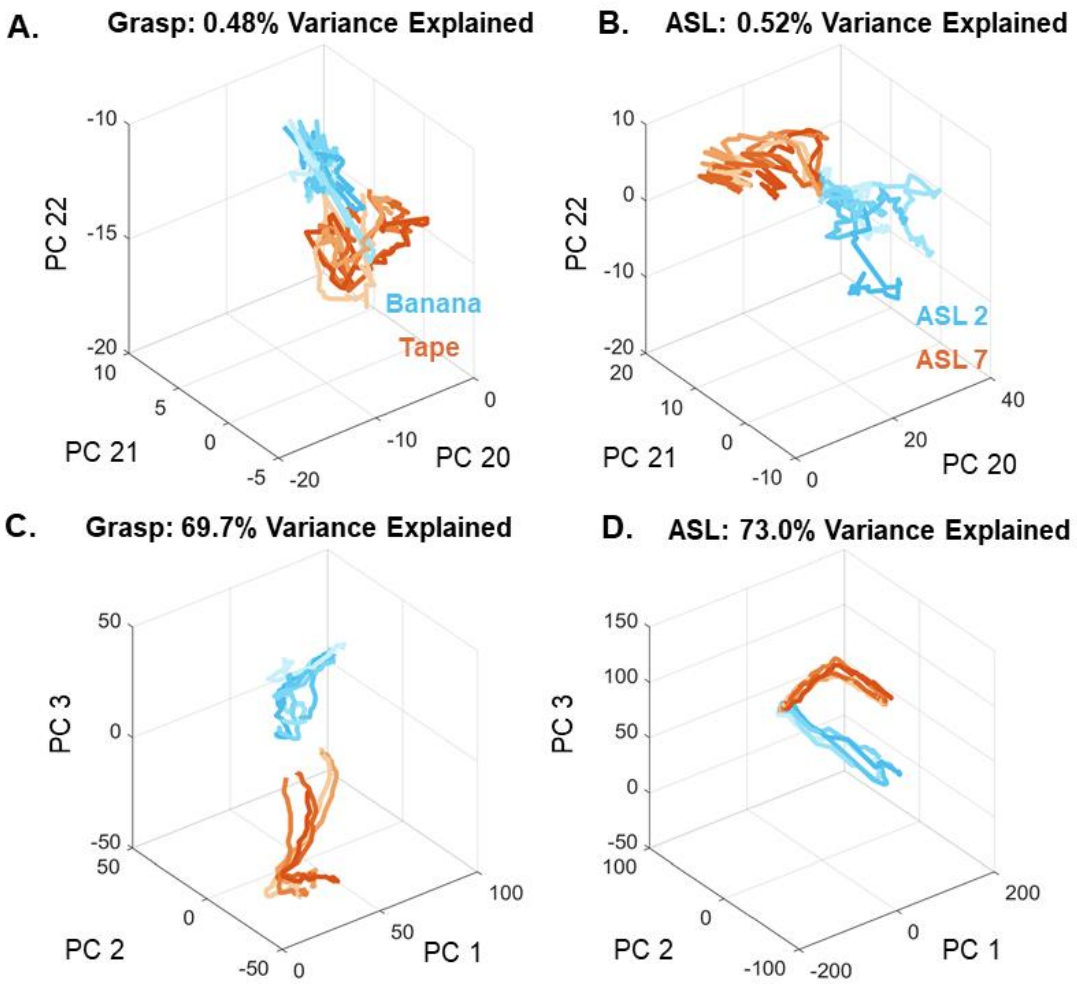

Figure 5. Object-specific kinematics in PC subspaces. A| Projection of the kinematics onto the subspace formed by PCs 21 through 23 for five grasps each of tape and banana. B| Projection of the kinematics for five repeated signs each of "two" and "seven" in ASL onto PCs 21 through 23. C| Projection of the kinematics onto PCs 1 through 3 for the conditions shown in panel A. D| Projection of the kinematics onto PCs 1 through 3 for the conditions shown in panel B. In all panels, separate objects and signs are indicated by color, and different trials are indicated by traces of different brightness.

To quantify the degree to which kinematics differed across conditions, we classified objects or letters using progressively reduced kinematic subspaces. We found that classification accuracy was above chance even after all but the last few PCs had been removed, and that high performance was achieved

even with PCs which collectively accounted for less than one percent of the variance in kinematics

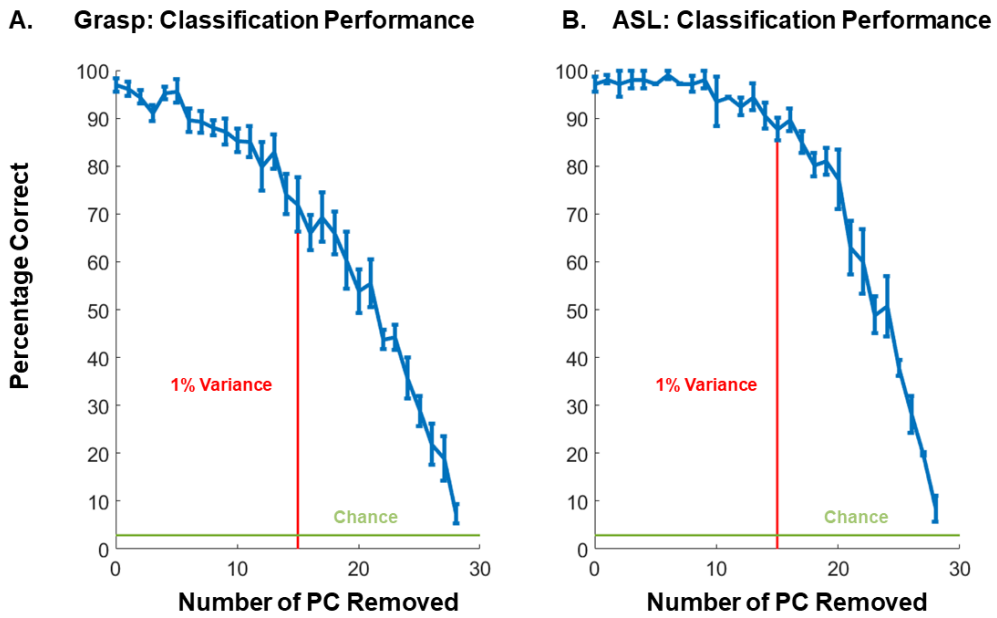

Figure 6. Classification of condition (object, sign) based on kinematics in progressively reduced subspaces. A| Grasp classification performance after progressively removing PCs, from high variance to low. B| ASL classification performance with reduced kinematic subspaces. Vertical lines denote the PC beyond which less than 1% of the variance is accounted for. Note that objects and letters can be classified accurately based on just a handful of high-variance PCs (**Supplementary Figure 4**).

(**Figure 6 A, B**). A similar result was obtained when progressively removing LDA dimensions rather than PCs (**Supplementary Figure 2**). Results from these classification analyses are thus inconsistent with the hypothesis that low-variance PCs reflect motor or measurement noise. Rather, these PCs seem to reflect subtle dimensions of movement that are under volitional control and contribute to the exquisitely precise pre-shaping of the hand to an object or to the detailed execution of a complex conformation as is required in ASL.

Discussion

The structure of hand kinematics depends on the manual behavior

Examination of time-varying human hand postures revealed substantial differences in the structure of the kinematics across some tasks but not others. Specifically, grasping and ASL elicited hand movements with similar patterns of inter-joint correlations whereas typing yielded very different patterns. In fact, the kinematic structure was more similar across subjects than it was across tasks. This result challenges the notion that hand movements are constrained to a universal lower-dimensional manifold regardless of the behavior [9,19,23]. Indeed, ours is only a replication of the finding that different tasks involve different kinematic manifolds [11,12,35].

Volitional hand movements are high dimensional

That the correlational structure of hand movements changes substantially across tasks argues against the hypothesis that hand movements universally occupy some lower dimensional manifold, reflecting a neural strategy to simplify hand control. However, one possibility is that hand movements are low-dimensional within any one task and that the manifold changes from task to task. Indeed, one hypothesis derived from (but not necessarily entailed by) optimal feedback control theory stipulates that the CNS defines low-dimensional manifolds of control to satisfy movement goals on a task-by-task basis, with motor noise being preferentially shunted into dimensions outside of such manifolds [36–38]. According to this hypothesis, the readout of grip type or ASL letter should be restricted to a lower-dimensional manifold than that afforded by the biomechanics of the hand. In other words, even though grasp and ASL occupy a different manifold than does typing, those different manifolds should, themselves, be low-dimensional. However, classification based on subsets of principal components revealed that high-rank (e.g., 20-22) PCs contain substantial object- and ASL sign-specific information. Indeed, kinematic trajectories projected on high-rank PCs were highly consistent within condition and different across conditions (**Supplementary Figure 1**). Such task-relevant information would not be present if such dimensions simply reflected motor or measurement noises, suggesting instead that volitionally controlled hand movements occupy a high dimensional space.

The possibility remains that nonlinear dimensionality reduction would reveal that hand kinematics indeed occupy a low-dimensional manifold. However, linear approaches, including PCA, have been previously shown to yield more efficient and reliable manifolds than do non-linear ones [39]. While the informativeness (condition dependence) of low-variance dimensions in non-linear manifolds was not probed in these previous studies, there is no reason to believe that a less efficient manifold in terms of explained variance would yield a more efficient representation in terms of informativeness.

Implications for the interpretation of synergies

High-dimensional kinematics do not imply wholly unconstrained control of the hand. Indeed, single-finger movements attempted by monkeys [40] and humans [41] are never perfectly individuated: They comprise incidental movements of the other digits arising in part from co-contraction of musculature associated with other digits. Recently, the analysis of the constraints imposed on neural activity in primary motor cortex (M1) revealed that activity patterns are constrained not only to a particular linear subspace [42], but also to a particular bounded region, or "repertoire," within that subspace [43]. The known constraints imposed on volitional hand movements might be better explained in terms of a bounded repertoire within a high-dimensional subspace rather than an unbounded repertoire within a low-dimensional subspace.

Whether the high-dimensional structure of hand movements argues against the notion of low-dimensional motor control in general remains to be seen. Indeed, numerous reports suggest that kinematics of the hand are especially high-dimensional relative to kinematics of other effectors [16,44–46]. Moreover, a subdivision of primate M1 appears to have direct access to muscles, particularly muscles of the hand [6], which might constitute anatomical evidence for the special nature of hand motor control. A common counterargument, one supporting low-dimensional motor control, is that the brain needs to simplify the problem of controlling a complex effector such as a hand to solve it. However, recent advances in large scale neuronal recordings suggest that this notion is fundamentally misguided. Indeed, sensory representations of natural scenes in primary visual cortex

eclipse 500 dimensions [47], an order of magnitude more than the implied representations of hand postures. Nonetheless, visual percepts are highly intuitive and complex objects can be identified accurately, rapidly, and effortlessly [48]. In comparison, motor control is positively straightfoward!

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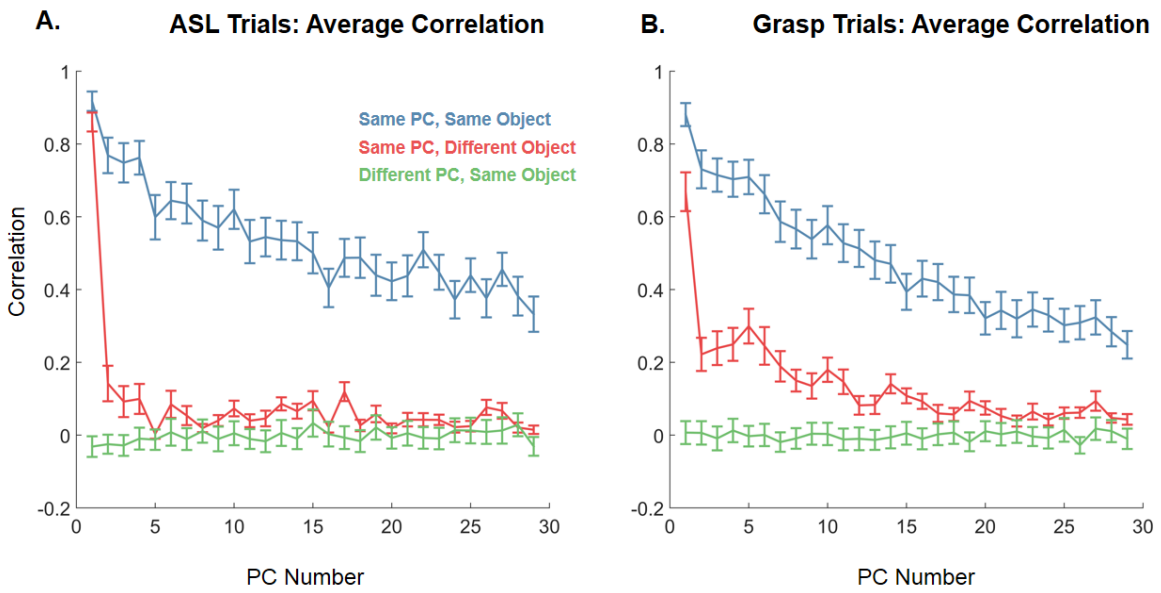
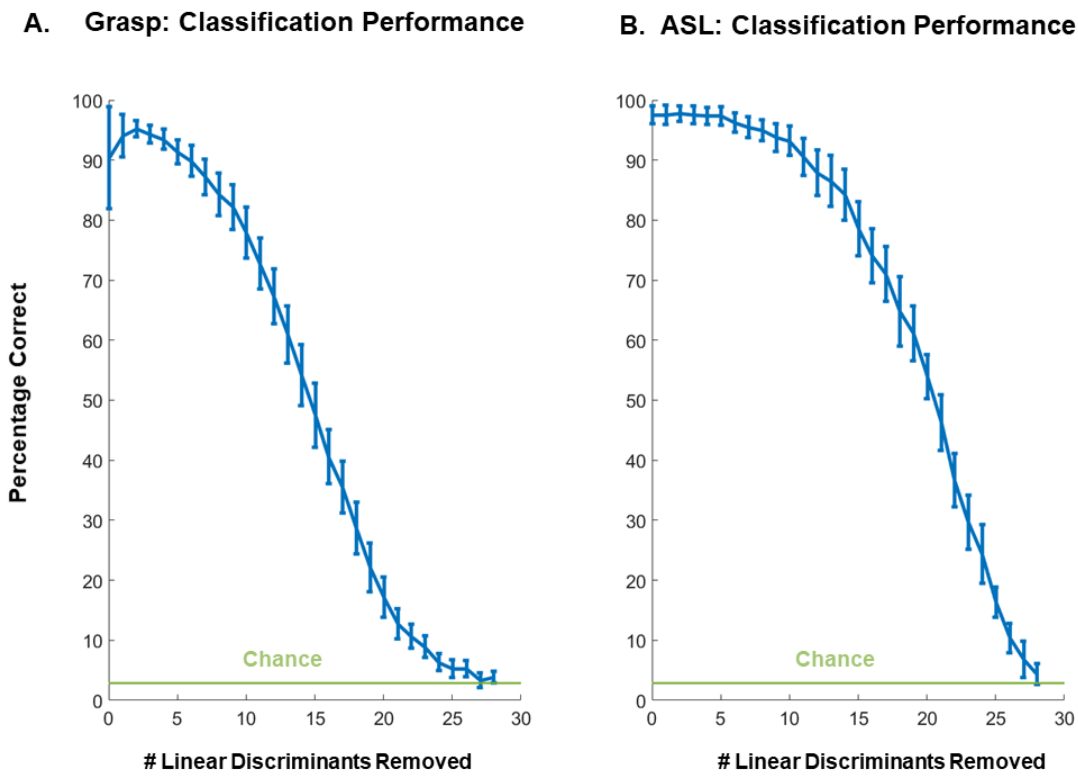
SUPPLEMENTARY FIGURES



Supplementary Figure 1 Consistency of kinematics projected onto each PC. A| Mean correlation coefficient between kinematics for different trials of the same object projected onto the same PC (blue), for different trials of the same object projected onto different PCs (green), and for trials from different objects projected onto the same PCs (red). The within-object, within-PC correlations are systematically higher than their shuffled counterparts. B| Same analysis for ASL trials.



Supplementary Figure 2 Classification performance with a progressively reduced number of linear discriminants. A| Classification accuracy for grasped objects as the dimensions identified by LDA were removed based on their respective Fisher's coefficient (ratio of between class variance to within class variance), from highest to lowest. B| Classification accuracy of ASL posture as LDA dimensions are removed in the same way.

A. Passage 1: Right Hand Words

lumpy humpy imply nigh jupon ovum; hoping goblin logy limn boil kiln phonily moping plumy junk limb, jumpily lion hump jump moving; knob humping holing homily' bony plum hominy boing ugly buoying puny hunky bulking' juking glim; joking uplink bilgy gonium holy gumbo limo bough mingy milky long young linkup; hymn hypo jumping.

globin loving kilo' bulky plink upon nymph numb moil homing punk; buoy gulp gimpy poky blip humbly honky plough goby ping; gluon bunko gunk yolk inly plying vying bilk opium login bung? Hulky glop ploy plonk king bumping, jumpy glyph bulgy.

Milk monk john bogy yogh, gunky liny plumb glum hunk, ignobly bigly pong bumpy jingo poking lying blink nobly? Lump khoum. Vino lymph phylum joying blog unholy pink junky jokily glom hulking' only bulk pylon milo moly hilum gink poly; bunk join bluing oily yoni ling nimbly unhip. Lough knop puling limy hokum vinyl limp; viol bijou bump bonk buying pony plunk; honk blimp numbly plug' umbo nympho glob.

Bumpkin lumping pinkly hypoing' loping, lubing gumboil jingly holm link pokily, umping muni, lungi bingo hulk kingly, oink mogul impugn pinky hung gimp, pigmy ghoul lung hyping. Phony jumbo pluming; yoking loin bumpily limbo linkboy.

B. Passage 2: Normal Words

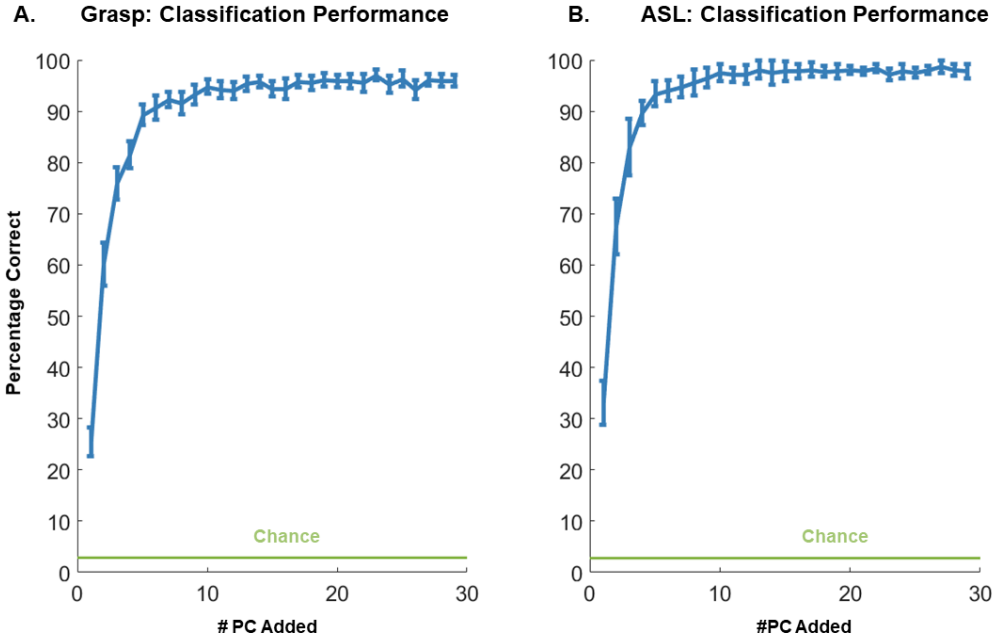
The neocortex, also called the neopallium and isocortex, is the part of the mammalian brain involved in higher-order brain functions such as sensory peas sensory perception, cognition and generation of motor commands, spatial reasoning and language. The neocortex contains both excitatory (~80%) and inhibitory (~20%) neurons, named for their effect on other neurons.

The structure of the neocortex is relatively uniform (hence the alternative names "iso-" and "homotypic" cortex), consisting of six horizontal layers segregated principally by cell type and neuronal connections. However, there are many exceptions to this uniformity; for example, layer IV is small or missing in primary motor cortex.

There is some canonical circuitry within the cortex; for example, pyramidal neurons in the upper layers II and III project their axons to other areas of neocortex, while those in the deeper layers V and VI often project out of the cortex, e.g. to the thalamus, brainstem, and spinal cord.

Neurons in layer IV receive the majority of the synaptic connections from outside the cortex (mostly from thalamus), and themselves make short-range, local connections to other cortical layers. Thus, layer IV is the main recipient of incoming sensory information and distributes it to the other layers for further processing.

Supplementary Figure 3 Text used in the typing task. A| Collection of words that only used letters to the right of the "Y-G-B" boundary on an English keyboard. Words are arranged in paragraph-like structure with punctuations. B| Passage taken from the Wikipedia page of neocortex (https://en.wikipedia.org/wiki/Neocortex), which used a variety of common and uncommon words.



Supplementary Figure 4. Classification performance with progressively larger subspaces. A| Classification performance for grasped objects as PCs are added in descending order of variance explained (blue curve). B| Classification performance for ASL letters vs. number of PCs. Green line denotes chance performance.